The Reproductive Cycles of True Firs

BC
Ministry of Forests

86-06194/

The Reproductive Cycles of True Firs

The Reproductive Cycles of True Firs

by
John N. Owens
and
Marje Molder

Biology Department
University of Victoria
Victoria, British Columbia

Province of British Columbia
Ministry of Forests

Canadian Cataloguing in Publication Data

Owens, John N., 1936-
The reproductive cycles of true firs

Includes bibliographical references.
ISBN 0-7718-8459-1

1. Fir - British Columbia. 2. Conifers - British Columbia - Reproduction. I. Molder, Marje, 1945- II. British Columbia. Ministry of Forests. III. Title.

QK494.5.P660935 1985 585'.20416 C85-092054-X

© 1985 Province of British Columbia
Published by the
Information Services Branch
Ministry of Forests
1450 Government St.,
Victoria, B.C.
V8W 3E7

Copies of this and other Ministry of Forests' titles are available from
Queen's Printer Publications,
Parliament Buildings,
Victoria, B.C. V8V 4R6

PREFACE

British Columbia has 25 native conifer species, of which 15 are commercially important and scheduled for reforestation. Tree improvement programs for four of these species are now under way and programs for several other species are planned. A necessary prerequisite for extensive reforestation and tree improvement programs is a complete understanding of the reproductive cycle of each species.

Until 1970, Douglas-fir was the only native species for which the complete reproductive cycle was known. Since that time, studies of the reproductive cycles have been completed for 13 of the other commercially important conifers. These studies include descriptions of vegetative bud and shoot development as they relate to cone initiation, the time and method of cone initiation, predormant and postdormant cone-bud development, pollen development, pollination, and embryo and seed development. Although these studies provide essential details of the reproductive cycles, a more general description of all aspects of the reproductive cycle of particular species is frequently requested.

This request has resulted in a series of short books concerning the reproductive cycles of several conifers. Serving as ready references for foresters and others concerned with seed production and tree improvement, these books will explain the complete reproductive cycle; provide useful guidelines for cone-induction studies; assist in forecasting pollen and seed production; enable more effective pollination; and provide some clues to the causes of poor seed production. In addition, such information should be useful to students of forestry and biology at universities, technical schools, and high schools.

This book, *The Reproductive Cycles of True Firs*, is not meant to include a complete literature review. Only the most pertinent or accessible references are cited and listed, providing a source for numerous related reports.

ACKNOWLEDGEMENTS

Financial support was provided by the British Columbia Ministry of Forests, Research and Silviculture Branches and the Natural Sciences and Engineering Research Council of Canada, Grant A-1982.

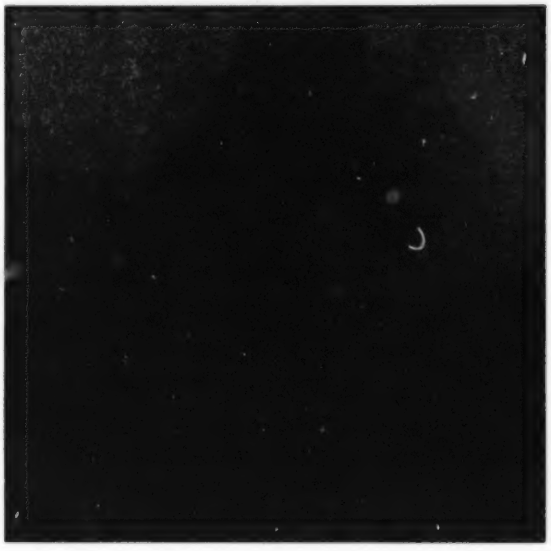
Gratitude is extended to Margaret D. Blake and Sheila J. Simpson for their scanning electron microscopy and excellent technical assistance; to Tom Gore for photographic assistance; and to Oldriska Ceska for art work.

We also wish to thank J. Konishi, M. Crown, S.D. Ross, and J.E. Webber of the B.C. Ministry of Forests for reviewing the manuscript, and the staff at the B.C. Ministry of Forests, Seed Centre, Duncan, B.C., for their valuable information and helpful suggestions.

TABLE OF CONTENTS

Preface v
Acknowledgements v
Introduction 7
Distribution and Taxonomy 7
Economic Importance 9
Reproductive Phenology 9
Reproductive Potential 10
Vegetative Bud and Shoot Development 11
Differentiation of Bud Types 12
Pathways of Bud Development 13
Enhancing Cone-Bud Differentiation 15
Identification of Buds 17
Forecasting Cone Crops 18
Pollen-Cone Development 19
Seed-Cone Development 21
Pollination 21
Ovule Development 23
Fertilization 25
Embryo Development 26
Seed Development 28
Cone Maturation, Seed Release, and Regeneration 30
Cone Collection, Seed Extraction, Storage, and Germination 31
The Seedling 32
Summary 33
References 34

The Reproductive Cycles of True Firs



Introduction

The true firs are a genus *(Abies)* within the Pinaceae consisting of about 40 species, all native to the Northern Hemisphere. Nine (Hosie 1969) to 12 species (Von Rudloff 1975) grow in North America, four in Canada. These four are balsam fir (*Abies balsamea* (L.) Mill.), which grows in all provinces except British Columbia; and alpine fir (*A. lasiocarpa* (Hook.) Nutt.), amabilis fir (*A. amabilis* (Dougl.) Forbes), and grand fir (*A. grandis* (Dougl.) Lindl.), which have more limited distributions in the west (Fowells (compiler) 1965; Hosie 1969). Only the latter three species, which are native to British Columbia, will be considered in this report. Three other North American species, white fir (*A. concolor* (Gord. and Glend.) Lindl.), Shasta fir (*A. magnifica* A. Murr.), and noble fir (*A. procera* Rehd.), are often planted as ornamentals. Interest has been shown in noble fir as a species to be used for reforestation in British Columbia. A fourth common ornamental is Spanish fir (*A. pinsapa*) from southern Spain (Dallimore and Jackson 1966; Hosie 1969).

The true firs are distinct from other native conifers in that the cylindrical or egg-shaped seed cones (Figs. 1-3) remain in an upright position in the topmost branches. The upright cone characteristic is also shared by the true cedars (*Cedrus*) which are common ornamentals. Seed cones mature in one growing season and at maturity the cone scales are shed, often with two attached seeds, each with a large seed wing. The true firs are stately evergreen trees with narrow pyramidal crowns and regularly whorled, horizontally spread branches. The leaves are flat, with a twisted base and no stalk. Leaves usually form two rows along the twig on lower branches. Upper branches have leaves curved upward and branches are less flattened. Buds are resinous in most species. The bark of young trees is smooth and thin with resin blisters but becomes scaly or thick and furrowed in older trees (Fowells (compiler) 1965; Hosie 1969).

Recent studies of leaf and twig oils (volatile terpenes) (Hunt and Von Rudloff 1974, 1979; Von Rudloff 1975, 1976; Von Rudloff and Hunt 1977), flavenoid compounds, and morphological features (Parker *et al.* 1979) of several *Abies* species have increased our understanding of the taxonomy, geographic distribution, and possible hybridization of species within the genus *Abies* in North America.

Distribution and Taxonomy

Alpine fir (Fig. 1) is one of the most widely distributed conifers in British Columbia (Fig. 4). It occurs in the Subalpine Forest Region and parts of the Boreal Forest Region at elevations from 600 m to 2100 m. It is distributed from southern Alaska through

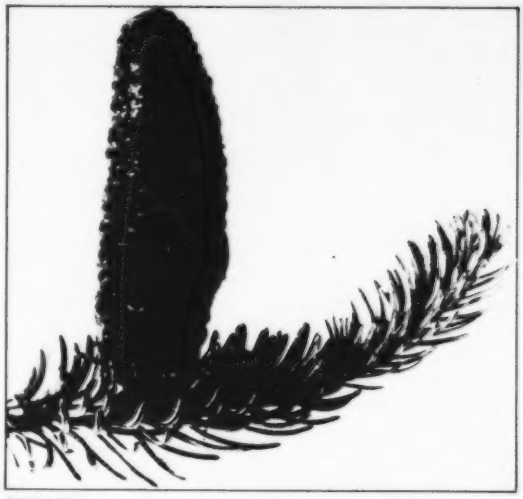


FIGURE 1. Alpine fir branch and cone. (X 0.5)

much of the southern Yukon Territory, southward through most of the British Columbia interior and into western Alberta. In the United States alpine fir extends southward in the Cascade Mountains into Oregon and in the Rocky Mountains into Arizona. It occurs at higher elevations on eastern slopes of coastal British Columbia and on Vancouver Island, but at lower elevations in the Interior (Fowells (compiler) 1965; Hosie 1969).

Alpine fir overlaps with *A. balsamea* in central Alberta where introgression takes place (Hunt and Von Rudloff 1979). Similarities in leaf-oil terpenes indicate that *A. lasiocarpa* and *A. balsamea* may have originated from a common ancestor in western North America, until this parent species contracted into separate groups during more recent ice ages. During this separation, *A. lasiocarpa* and *A. balsamea* became more distinct but still hybridized when their range overlapped. The small stands of fir in the prairie provinces may be progeny from this past hybridization. Consequently, some authors prefer to consider them as a single species, whereas others prefer to keep them as separate species (Hunt and Von Rudloff 1974). Early taxonomists treated our present *A. lasiocarpa* as two species, the coastal *A. lasiocarpa* and an interior *A. bifolia* (Murray 1863). Recent evidence based on volatile oils of leaves supports this separation, although other interpretations do not recognize *A. bifolia* as a separate species but rather as an eastern variety of *A. lasiocarpa* (Parker and Maze 1984), or *A. lasiocarpa* is considered to be a variety of *A. balsamea* (Hunt and Von Rudloff 1979). The controversy over the taxonomy of alpine fir is still unsettled (Hunt and Von Rudloff 1979). To be consistent with commonly used references (Fowells (compiler) 1965; Hosie 1969), alpine fir will be treated here as a single species (*A. lasiocarpa*) with coastal and interior forms. Its distribution is shown in Figure 4.

Amabilis fir (Fig. 2) occurs in coastal regions from southern Alaska to the southern part of British

FIGURE 2. Amabilis fir branch and cone. (X 0.3)

Columbia. It occurs over most of Vancouver Island, in the Olympic Mountains of Washington, and in the northern coastal regions of Oregon. It extends southward in the Cascade Mountains to northern California (Fig. 5). It grows at sea level in the northern part of its range, and up to 1500 m elevation in southern British Columbia and in the Pacific Northwest (Fowells (compiler) 1965; Hosie 1969).

The range of amabilis fir overlaps with that of alpine fir at higher elevations and with grand fir at lower elevations (Figs. 4-6). In the southern part of its distribution in the Cascade Mountains, its range also overlaps with that of noble fir (*A. procera* Rehd.), white fir, and California red fir (Fowells (compiler) 1965). Interspecific hybrids have not been reported between amabilis fir and any of these firs (Von Rudloff and Hunt 1977).

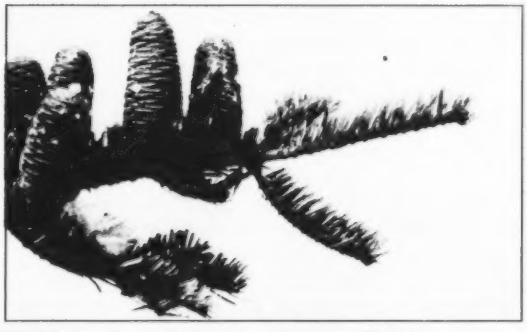


FIGURE 3. Grand fir branch and cones. (X 0.2)

Grand fir (Fig. 3) has a very limited distribution in British Columbia (Fig. 6). It is a low-elevation species, usually below 450 m, and is common in valleys, along streams, and on low mountain slopes. It occurs on the east coast of Vancouver Island and the adjacent mainland. In the Interior it occurs south from the Okanagan and Kootenay lakes. It is widely distributed from the Cascade Mountains westward in Washington and northern Oregon, but occurs mostly west of the coastal mountains in southern Oregon and Northern California. It also extends southward in the Interior to central Idaho.

The diversity of *Abies* species and their extensive distribution in diverse habitats from sea level to subalpine regions in western North America makes it an important genus in the ecology and economy of this region.

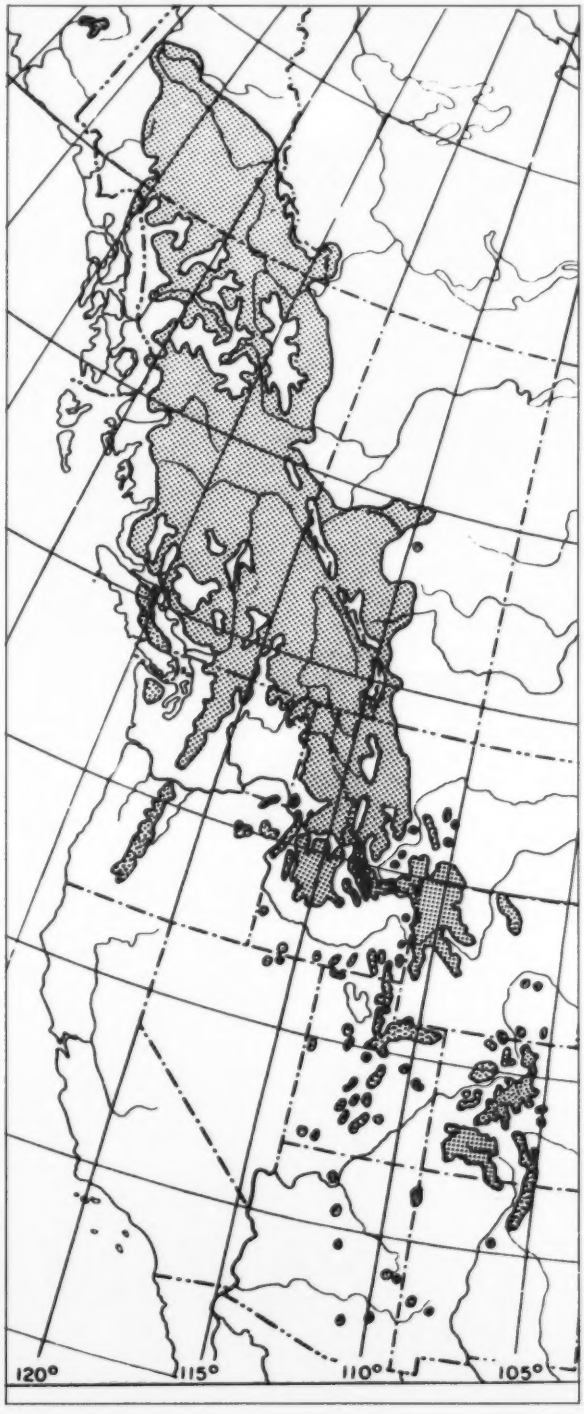


FIGURE 4. Distribution of alpine fir. (Redrawn from Fowells (compiler) 1965.)

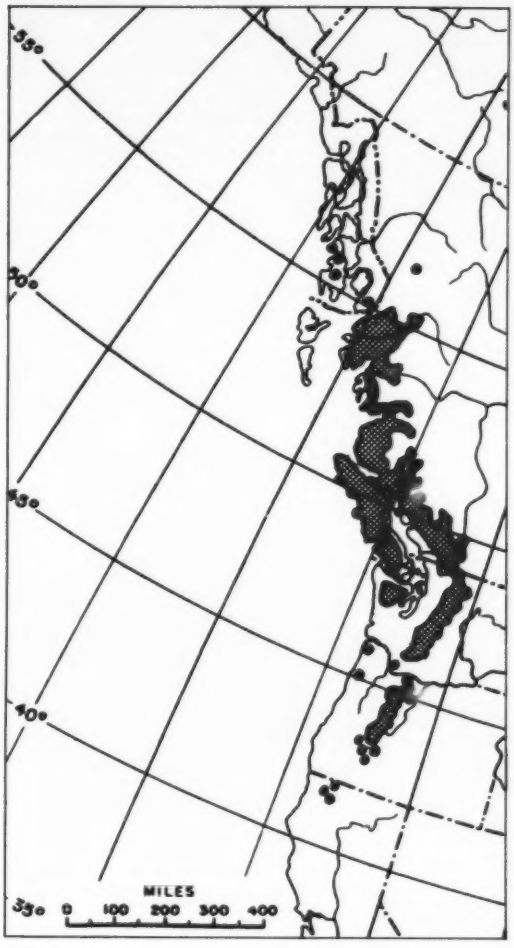


FIGURE 5. Distribution of amabilis fir. (Redrawn from Fowells (compiler) 1965.)

Economic Importance

The true firs, primarily subalpine and amabilis firs, are extensively harvested in British Columbia. In recent years, the true fir accounted for about 13% of tree species cut in British Columbia, ranking fifth behind spruces, lodgepole pine, Douglas-fir, and hemlocks. This harvest is almost equally split between coastal and interior firs but no clear distinction is made between species harvested. Amabilis fir in coastal regions, some subalpine fir in the mountains, and little grand fir are harvested. Alpine fir, because of its more extensive distribution in the Interior, is harvested most (B.C. Ministry of Forests 1982).

True firs are commonly intermixed with other local species and often they are cut and marketed without differentiation between species. The wood from true firs is similar but is considered inferior for lumber when compared to many associated species. Their most extensive use is for pulp. In some parts of Canada, the liquid from the resin blisters on the bark is collected and marketed under the name of "Canada balsam". Various leaf oils are also used in the manufacture of some medicinal products (Hosie 1969). Some true firs are used extensively for Christmas trees because of their symmetrical form and aromatic leaf oils.

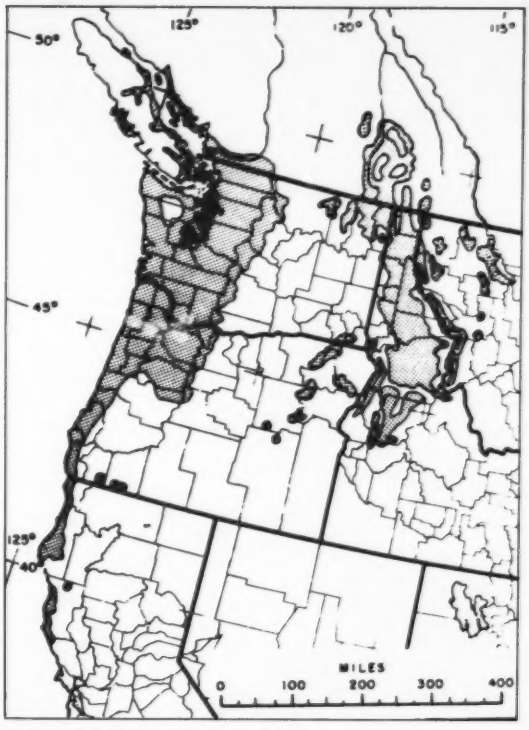


FIGURE 6. Distribution of grand fir. (Redrawn from Fowells (compiler) 1965.)

Infestations of the balsam woolly aphid (*Adelges piceae*) on true firs (Fowells (compiler) 1965) have resulted in restrictions on the transport of trees from infested zones in southern British Columbia, and have caused extensive damage to stands in the Pacific Northwest. An effective control for this forest pest has not yet been found. Fortunately, infestations have been restricted to southern British Columbia and have not extended into the vast distribution of true firs in the interior and north coastal regions[1].

Reproductive Phenology

The reproductive cycles of the true firs that have been studied (Miyake 1903; Hutchinson 1914; Powell

[1] Plant Protection Act, Order in Council 44, Approved and Ordered, January 7, 1977. Complete reference can be found in The British Columbia Gazette, Part II, January 18, 1977.

1970, 1974; Owens and Molder 1977a, 1977b, 1984; Singh and Owens 1981, 1982; Owens and Singh 1982; Owens 1984) are essentially the same in anatomical detail. The main difference is in the phenology, or chronology, of reproductive development, which may vary with the habitat. The phenology given here is that which would be found for interior alpine fir and coastal amabilis fir growing at moderate elevations in British Columbia (Fig. 7). This will be compared with the phenology of grand fir growing in low-elevation coastal regions. Some comparisons will also be made with balsam fir which has been extensively studied in eastern Canada (Miyake 1903; Powell 1970, 1974; Parker *et al.* 1979; Owens and Singh 1982; Parker and Maze 1984). It is recognized that the phenology will vary within a species at different elevations and latitudes and between the three native species. However, the sequence and details of reproductive development will remain the same and a single general description of the reproductive cycle is valid (Fig. 7).

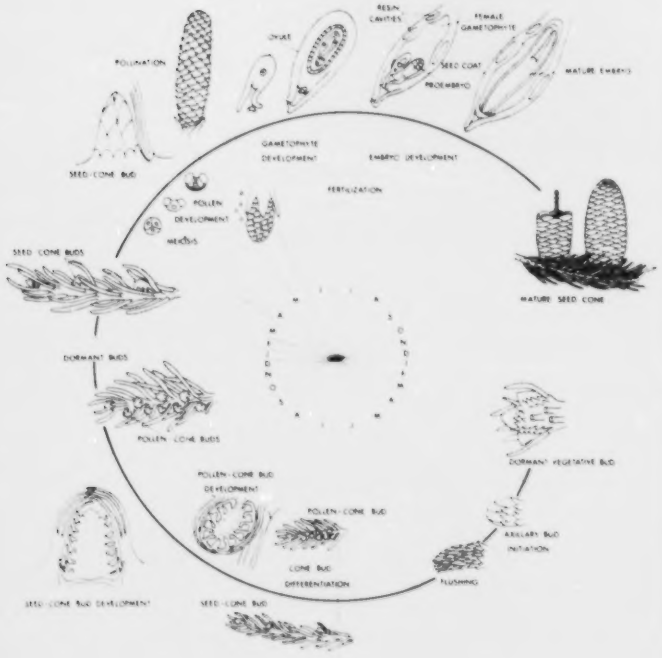


FIGURE 7. Reproduction phenology of alpine and amabilis firs.

Reproductive Potential

The true firs are generally considered to be moderate to poor cone and seed producers compared to other conifers. They have a long juvenile period when no cones are produced, and typically produce few cones, often with a low percentage of filled seed. Also, seed viability is quite variable. When seed cones are produced they are usually restricted to the uppermost whorls of the crown, making cone collection difficult. Also, cones must be collected early before the cone scales abscise and seeds are lost. Seed extraction is also more difficult than for other species and routine methods do not work for true firs. Because of these problems, seed procurement for reforestation is difficult and very costly. Clearly, an understanding of the complete reproductive cycles of each of the true firs will be essential to maximize seed production in seed orchards containing these species.

Alpine fir in British Columbia and many parts of the Pacific Northwest is generally ranked as a moderate to poor cone and seed producer because many trees often produce no or few cones per tree (less than 50), and there is generally low seed yield per cone (Franklin 1968; Owens and Singh 1982). However, at moderate elevations in the southern part of its range, alpine fir is considered to be a good seed producer, with good seed crops occurring every two to five years, and light crops in intervening years. Occasionally there are crop failures (Fowells (compiler) 1965; Dobbs *et al.* 1976). Seed cones are 6-12 cm long and average 150 seeds per cone. Percent germination of seeds is quite variable depending upon seed lot, ranging from 2 to 83% with an average of 30% for the interior form; and ranging from 21 to 66% with an average of 47%, for the coastal form.[1] Other reports (Franklin 1968) give an average germination of 38%. Seed cones may first appear on trees that are about 20 years old (Fowells (compiler) 1965; Dobbs *et al.* 1976; Eis and Craigdallie 1981) but pollen cones may not appear until trees are 35 years old (Eis and Craigdallie 1981).

Although limited information is available, amabilis fir appears to be similar to alpine fir in cone bearing age and frequency of cone crops (Franklin 1968; Dobbs *et al.* 1976). Usually few seed cones are borne per tree. Seed cones are larger than for the other true firs (Figs. 1-3) — 9-13 cm long — and bear about 400 seeds per cone. Seed germination averages 46% and may range from 1 to 77%.[2] Other reports (Franklin 1968) give an average of only 22%.

Grand fir is a moderate to poor cone producer and commonly does not produce more than 40 cones per tree (Fowells (compiler) 1965). However, individuals bearing over 500 cones per tree have been reported (Franklin 1968). Good cone crops occur at intervals of three years (Fowells (compiler) 1965) to five or six

[1] Plant Protection Act, Order in Council 44, Approved and Ordered, January 7, 1977. Complete reference can be found in The British Columbia Gazette, Part II, January 18, 1977.

[2] British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

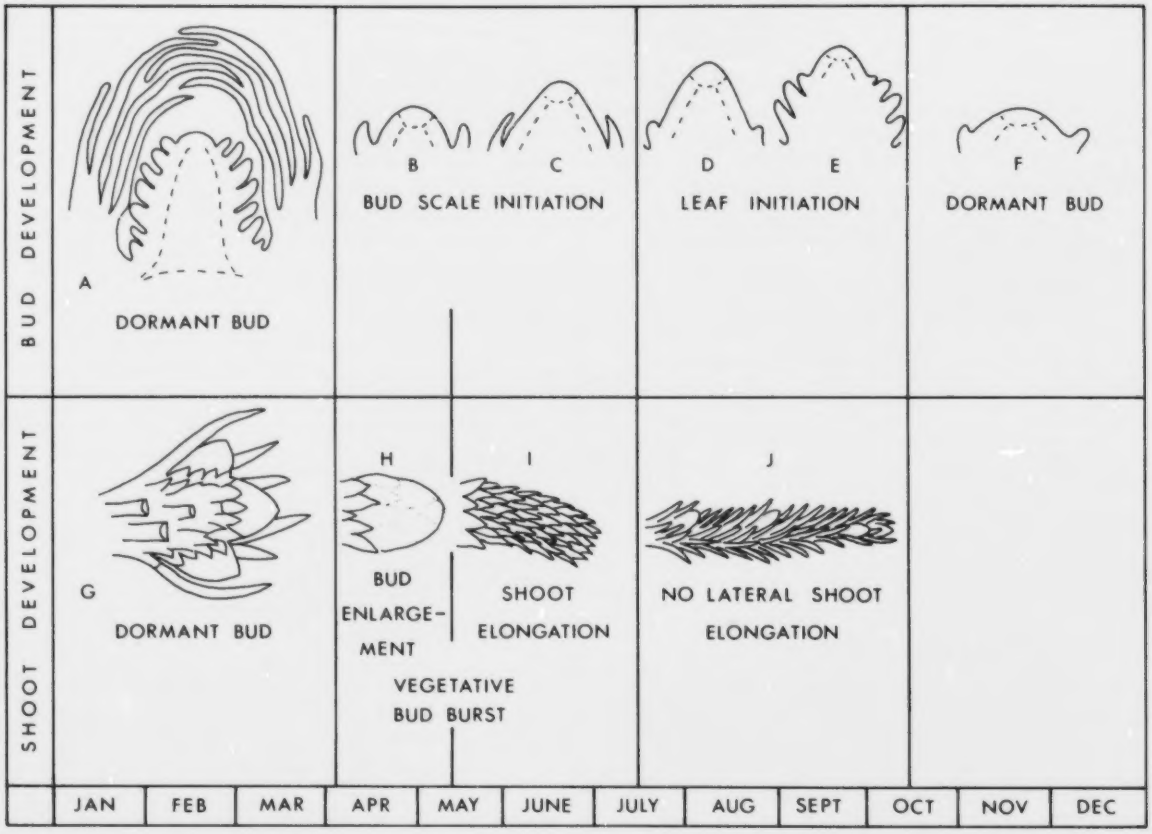


FIGURE 8. The phenology of vegetative bud and shoot development of alpine and amabilis firs.

years (Dobbs *et al.* 1976). Seed cones are 5-12 cm long and bear about 200 seeds per cone. Seed germination averages 69% and may range from 37 to 93%[1]. Other reports give a much lower average germination of 28% (Franklin 1968). Seed cones first appear on trees that are approximately 20 years old but, as in other true firs, production increases with age (Fowells (compiler) 1965).

The wide distribution and economic importance of alpine and amabilis firs in British Columbia make them valuable for reforestation. Grand fir may also be suitable for many low-elevation sites in southern British Columbia. Extensive reforestation requires a constant supply of high quality, yet economical, seed. In response to this need, genetic tree improvement programs and seed orchards will be established for at least some true firs. This will require a thorough understanding of the complete reproductive cycle of each species. This must include the important events during the 15 months from the time of cone initiation in the summer, pollination of these cones the following spring, through fertilization and embryo development that summer until seed is mature and shed in the fall of the year the cones were pollinated (Fig. 7).

[1] British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

Vegetative Bud and Shoot Development

Vegetative bud and shoot development are similar in alpine, amabilis, and grand firs, but the phenology varies with latitude and elevation (Owens and Molder 1977a; Owens and Singh 1982; Owens 1984). Trees in northern or high-elevation regions begin development later in the spring and stop development earlier in the fall than trees in southern or low-elevation regions. However, developmental events during the summer, or middle of the growth cycle, occur at about the same time in the three species. A typical example of moderate elevation coastal amabilis fir and lower elevation interior alpine fir is shown in Figure 8. The growing season for coastal grand fir may begin as much as one month earlier in the spring and continue one month longer in the fall. Because cone buds are initiated on the elongating lateral shoots that develop from the vegetative bud, it is important to understand vegetative bud and shoot development.

The appearance of vegetative buds and their internal structure is similar in the three species. Terminal vegetative buds on lateral branches are usually subtended by one or more lateral vegetative buds in a whorl at the base of the terminal bud (Fig.

FIGURE 9. Dormant vegetative terminal (T) and subterminal (S) axillary buds of alpine fir. (X 8)

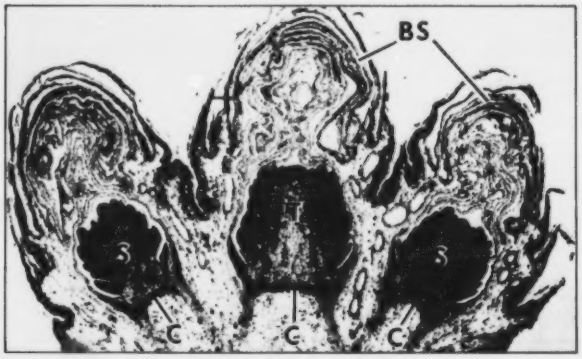


FIGURE 10. Median longitudinal section of dormant vegetative terminal (T) and subterminal (S) axillary buds of alpine fir showing bud scales (BS), crown regions (C) and embryonic shoots. (X 12)

FIGURE 11. Scanning electron micrograph of a dormant vegetative shoot of alpine fir showing the apical meristem (A) and leaf (L) primordia. (X 32)

9). More lateral vegetative buds also occur further down the shoot. Terminal and lateral vegetative buds consist of outer (brown, leathery) bud scales and inner (cream, papery) bud scales enclosing the completely preformed and "telescoped" vegetative shoot (Fig. 10). This shoot bears all of the next season's embryonic leaves (leaf primordia) (Figs. 8*A*, 10).

Dormant vegetative buds are encased in a thick resinous coat, which is secreted by the bud scales (Fig. 9). Vegetative buds of alpine and amabilis fir begin growth in early April (Fig. 8) and those of coastal grand fir begin growth in late March (Owens and Molder 1977*a*; Owens and Singh 1982; Owens 1984). When vegetative bud growth begins, the telescoped shoot axis elongates, causing the bud to swell (Fig. 8*H*) and then burst (flush) through the bud scales (Fig. 8*I*). This is followed by a period of rapid, then slow, shoot elongation (Fig. 8*J*) when shoot and leaf tissues mature and the next year's buds complete development.

During vegetative bud swelling, just before flushing, new lateral buds are initiated in the leaf axils (just above the juncture of the leaf primordium and the stem) of some leaf primordia (Fig. 13).

The apical meristems of the terminal and new lateral buds (Fig. 12) undergo a predictable sequence of developmental events (Fig. 8*B-F*) which correlate with shoot development (Fig. 8*H-J*). During shoot elongation the terminal and lateral apical meristems initiate a series of bud scales (Figs. 8*B-C*, 12). At the end of shoot elongation (about mid-July) the terminal apical meristems enlarge rapidly (Fig. 8*D*), then initiate a series of leaf primordia up the flanks of the apical meristem. The first two-thirds of the leaf primordia are initiated rapidly (Figs. 8*E*, 14), then the remaining one-third of the leaf primordia are initiated more slowly until the bud completes its development and becomes dormant in the fall (Figs. 8*A*, 11). Vegetative buds of alpine and amabilis firs become dormant in late October or early November and those of coastal grand fir become dormant in late November (Owens and Molder 1977*a*; Owens and Singh 1982; Owens 1984).

FIGURE 12. Scanning electron micrograph of a terminal apex during bud scale (BS) initiation. (X 80)

Differentiation of Bud Types

After the period of bud-scale initiation, axillary meristems may differentiate into one of three bud

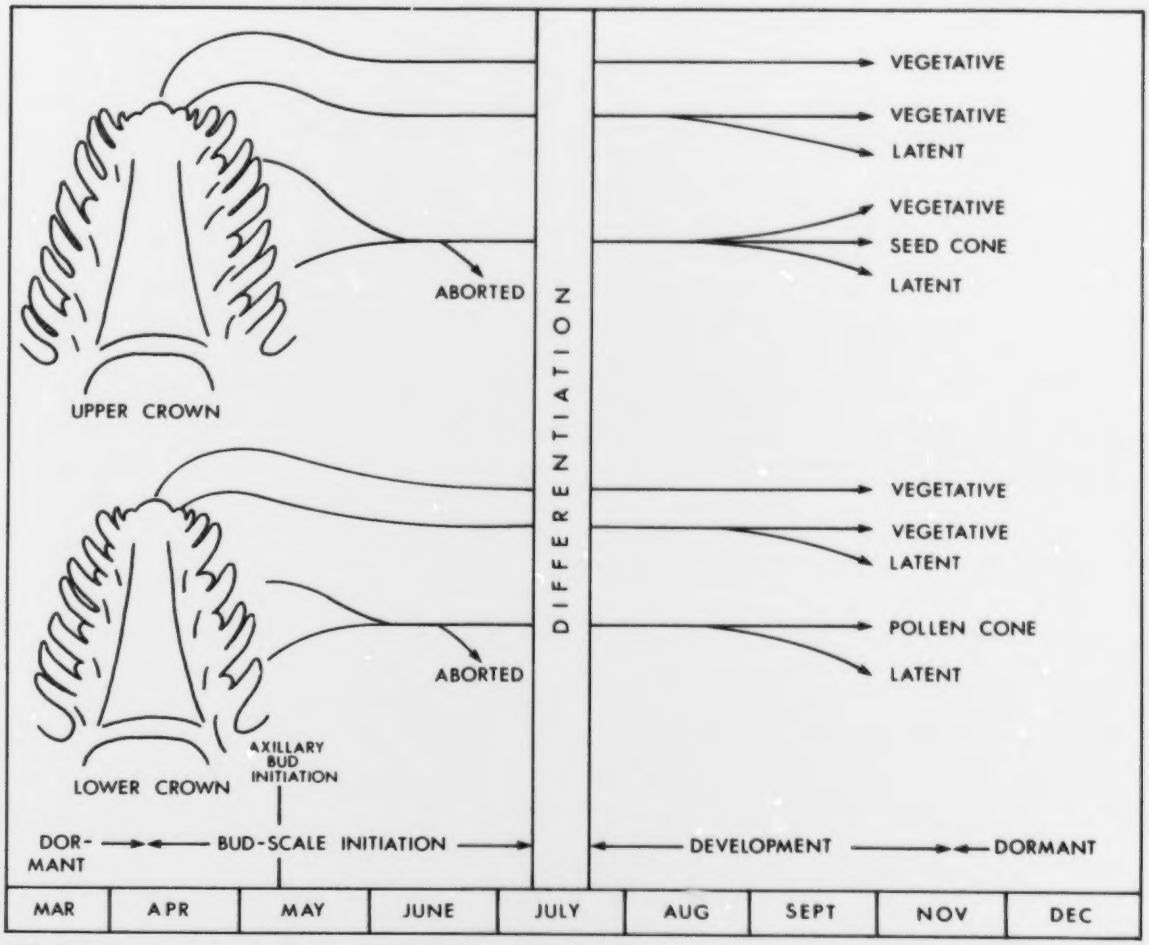


FIGURE 13. Pathways of axillary bud development on branches from lower and upper regions of the crown.

types — vegetative, seed-cone, or pollen-cone — or they may abort or become latent. At vegetative bud flush, axillary meristems consist only of a small mound of cells enclosed by a few bud scales. Just before shoot elongation is completed, in mid-July, some axillary apical meristems become more active than others. Their cells divide more frequently and they enlarge rapidly. These apical meristems develop into either seed-cone or pollen-cone buds. Other axillary apical meristems are less active, enlarge less, and develop into lateral vegetative buds as described above (Fig. 13).

The rate of development of other axillary apical meristems slows during bud-scale initiation and development may stop before all bud scales are initiated. If this occurs soon after the axillary buds are initiated, the axillary buds degenerate and leave no evidence of their previous existence. These are called aborted buds. Still other axillary apical meristems initiate most of their bud scales before development stops. These buds remain and are called latent buds (Fig. 13). They have not become determined as vegetative or reproductive buds when their growth stops. They consist of a small apical meristem surrounded by bud scales but with no additional primordia (Fig. 15) (Owens and Molder 1977*a*; Owens and Singh 1982; Owens 1984). Development in latent buds can often be stimulated by removal of the terminal vegetative bud on the twig. If this is done, they usually develop as vegetative buds. Many epicormic shoots (new shoots developing on older twigs) result because the inhibition of latent buds has been removed and they resume development.

Pathways of Bud Development

The abundance of cone buds in true firs is determined not so much by differences in the number of axillary buds initiated in the spring (since this varies little from year to year), but more by the pathways along which the axillary buds develop (Fig. 13). In a year when few cone buds develop, many of the axillary buds abort or become latent. In a year when

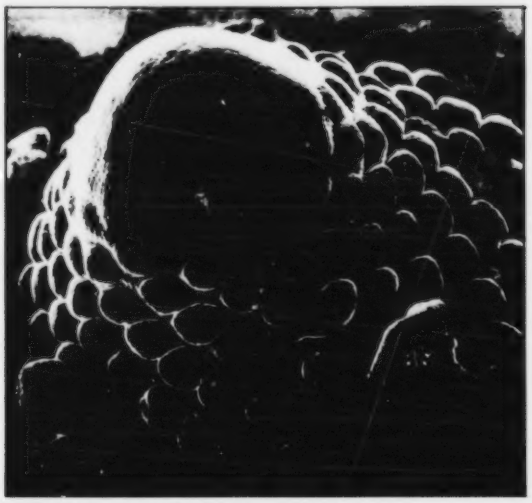


FIGURE 14. Scanning electron micrograph of a vegetative bud during leaf (L) initiation. Bud scales (BS) have been removed. (X 130)

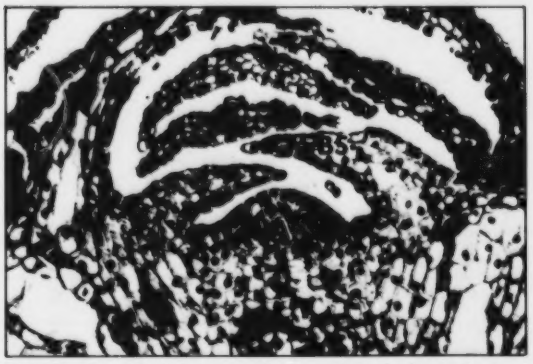


FIGURE 15. Median longitudinal section of a latent bud showing bud scales (BS) and small apical meristem (A). (X 100)

many cone buds develop, few axillary buds abort and many otherwise latent buds develop into cone buds, especially pollen-cone buds.

The position of the axillary bud on the shoot and of the shoot in the crown affects the pathway of axillary bud development. Seed-cone buds normally develop only on shoots in the upper region of the crown. They differentiate from axillary buds (Fig. 18) that were initiated usually on the upper surface of vigorous primary or secondary shoots (Fig. 23). They may occur all along the length of the new shoot, but are most common in the distal portion of the shoot. The more proximal axillary buds on the upper surface may become latent or form small vegetative buds. When conditions are favourable for cone-bud differentiation, nearly all axillary primordia on the upper surface of the twig will differentiate into seed-cone buds. When conditions are unfavourable for cone-bud differentiation, all of these buds will become latent or form small vegetative buds. In intermediate years, latent, vegetative, and seed-cone buds all will occur

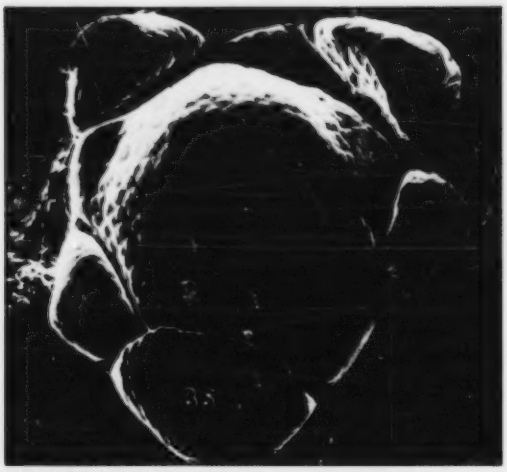


FIGURE 16. Scanning electron micrograph of a differentiating pollen-cone apex at the end of bud-scale (BS) initiation. (X 185)

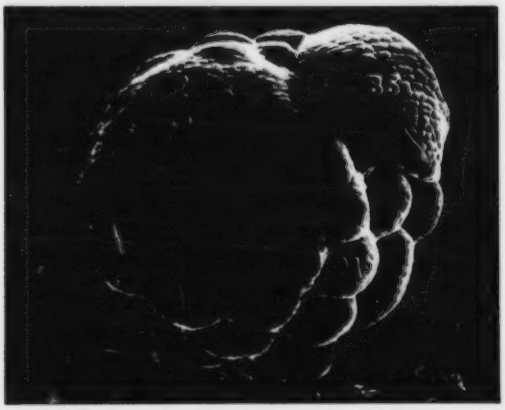


FIGURE 17. Scanning electron micrograph of a pollen-cone with most bud scales (BS) removed during microsporophyll (M) initiation. (X 120)

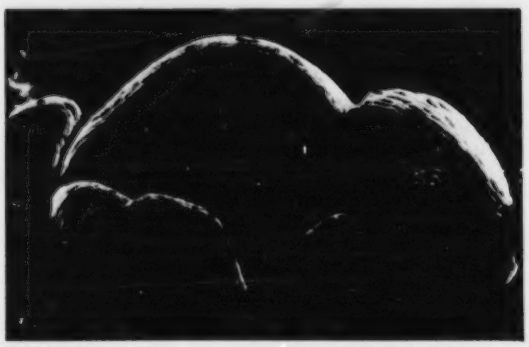


FIGURE 18. Scanning electron micrograph of a differentiating seed-cone apex at the end of bud scale (BS) initiation. (X 90)

on the same shoot, with the latent being most proximal and seed-cone buds being in the distal region of the

shoot. The distal axillary buds, located at the base of the terminal bud (Fig. 9), are always vegetative (Powell 1977*a*).

Pollen-cone buds normally develop on secondary or sometimes primary shoots having low vigour and are found in lower regions of the crown. Pollen-cone buds differentiate from axillary buds that were initiated in the axils of leaves on the sides and lower surface of the shoots (Fig. 16). When conditions are favourable for cone-bud differentiation, often most leaves will bear axillary pollen-cone buds. When conditions are unfavourable for cone-bud differentiation, many leaves will bear small latent buds. Usually, there will be both latent and pollen-cone buds in varying proportions. Latent buds may be scattered among the pollen-cone buds, but more commonly are abundant on proximal portions of the shoot.

FIGURE 19. Scanning electron micrograph of a seed cone with most bud scales (BS) removed during bract (B) initiation. (X 130)

Terminal buds in the true firs are nearly always vegetative. On rare occasions they may form seed-cone buds. Occasionally bisporangiate cone buds form which are part pollen-cone and part seed-cone bud (Eis 1970). Also, proliferated seed-cone buds may occur in which a vegetative bud develops at the tip of a seed cone (Eis 1970). These are anomalies which are of interest but are not significant in the reproductive potential of the species.

Enhancing Cone-Bud Differentiation

The internal factors that determine the pathway along which an axillary bud develops are unknown in true firs. The position of the developing bud on the

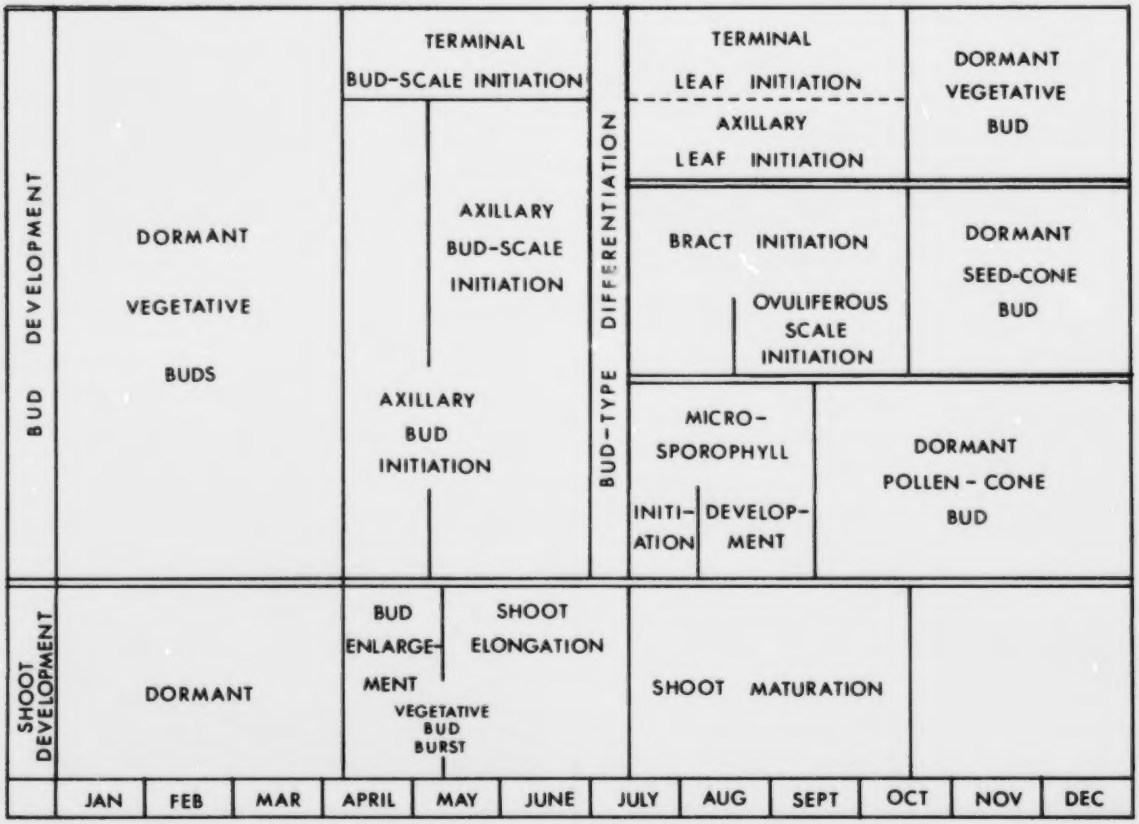


FIGURE 20. The time of bud differentiation and development in alpine and amabilis firs.

shoot and in the tree are important as well as the age of the tree, the genetic make-up of the tree, and numerous environmental factors. All of these interact to determine if axillary buds will develop at all and, if so, what their pathways of development will be.

Although cone induction in juvenile trees and cone enhancement in reproductively mature trees has been successful in several conifer genera, there are no reports of either for the true firs (Ross *et al.* 1983). This partly results from a lack of research on true firs but also indicates that these may be "difficult trees" for cone induction studies. This may be related to their long juvenile (non-reproductive) phase which normally lasts for 20 years or more.

The true firs appear to respond to the same environmental cues or factors that enhance cone-bud differentiation as do other conifers. These have their effect at or soon before the natural time of cone-bud differentiation, in the late spring or early summer of the year before these cones are pollinated (Fig. 7) (Owens and Molder 1977*a*; Owens and Singh 1982).

FIGURE 21. Dormant shoot from upper regions of the crown of alpine fir bearing vegetative axillary buds (V). (X 0.5)

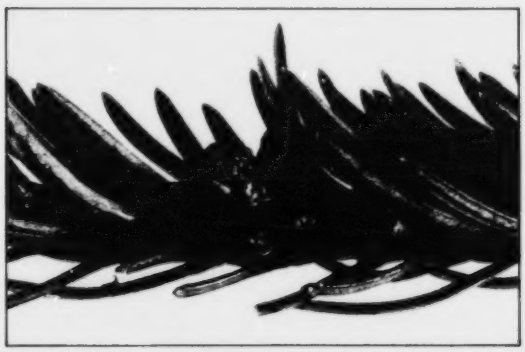


FIGURE 22. Dormant vegetative axillary buds (V) from alpine fir. (X 1.5)

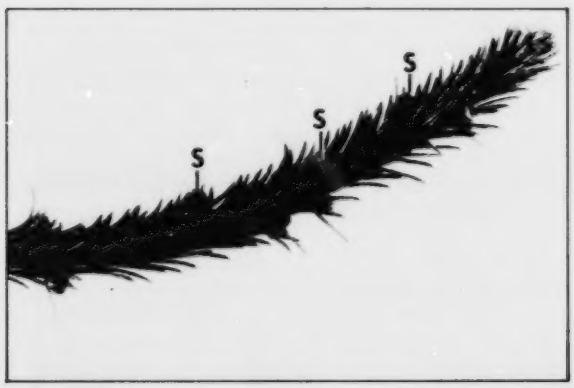


FIGURE 23. Dormant shoot from upper regions of the crown of alpine fir bearing seed-cone buds (S). (X 0.5)

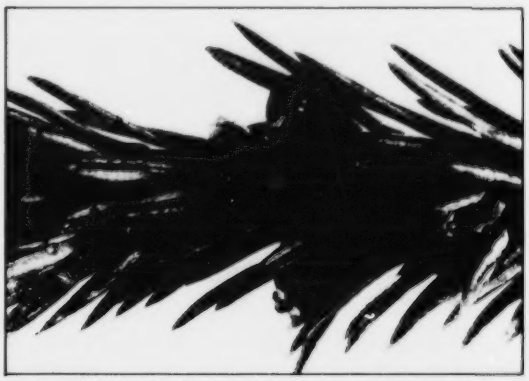


FIGURE 24. Dormant seed-cone buds (S) from alpine fir. (X 2)

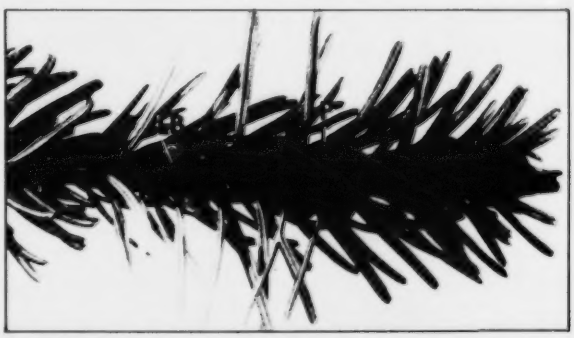


FIGURE 25. Dormant shoot from lower regions of the crown of amabilis fir bearing pollen-cone (P) and latent buds (LB). (X 1)

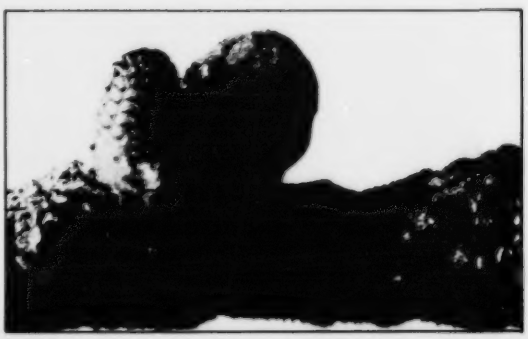
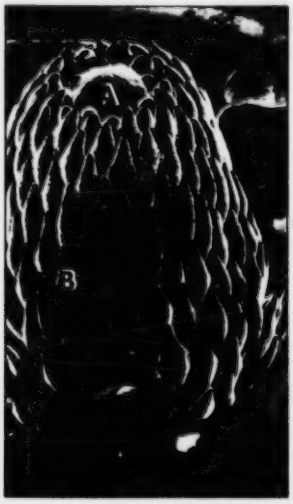


FIGURE 26. Dormant pollen-cone buds, one with bud scales removed, from amabilis fir. (X 6)

They include high temperatures, abundant sunshine, and low rainfall (Puritch 1972). Consequently, research on cone induction or enhancement in true firs should concentrate on the developmental period between vegetative bud flushing which occurs just after axillary bud initiation, and the end of lateral shoot elongation which coincides with the differentiation of buds.

It is possible that the cone-induction methods used successfully in other members of the Pinaceae may work on the true firs. These methods include physical stresses such as stem or branch girdling, strangulation or various forms of rootpruning, or otherwise limiting water uptake. Nitrate fertilization has also been successful in some species. The greatest effect appears to be obtained when one (or more) of these methods is combined with the application of the plant-growth regulator (hormone), gibberellin (Puritch 1972). In the Pinaceae the less polar gibberellins, especially a mixture of GA_4 and GA_7, have been used most successfully (Ross *et al.* 1983).

Early bud development and bud differentiation in true firs are very similar to that of certain other members of the Pinaceae (Owens 1973; Owens and Molder 1984*b*) where cone enhancement has been accomplished. Therefore, a similar approach might enhance cone production in the true firs.



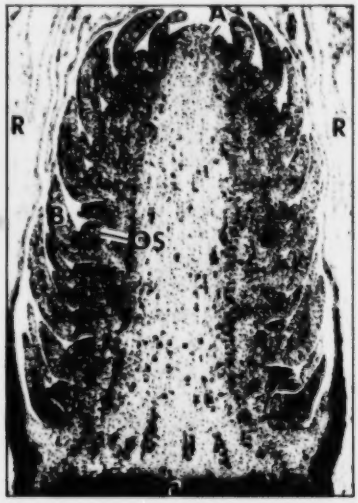


FIGURE 27. Scanning electron micrograph of a dormant seed cone after bud scales were removed. Apical meristem (A) and pointed bracts (B) are shown. (X 10)

FIGURE 28. Median longitudinal section of a dormant seed cone recessed in a deep receptacle (R). The apical meristem (A), bracts (B), ovuliferous scales (OS), and crown region (C) are shown. (X 12)

Identification of Buds

Vegetative buds initiate a spiral series of leaf primordia up the flanks of the apex during the summer and fall (Fig. 14). By mid- or late fall, all leaf primordia have been initiated (Fig. 11), a crown region has developed at the base of the bud (Fig. 10), and the vegetative terminal and lateral buds become dormant. No apical meristems are initiated in axils of leaves before dormancy. Dormant vegetative buds of all three species are broadly conical, brown, and encased by a thick layer of resin. Lateral buds have about 25 bud scales and terminal buds have about 40. The distal lateral buds, immediately subjacent to the terminal vegetative buds, are encased by a common resin coating (Figs. 9, 10). Vegetative buds are deeply buried in the broad receptacle to which the bud scales attach (Fig. 10). Vegetative lateral buds further down the shoot are often less buried in a receptacle and the broad receptacle may form a ridge around the base of smaller vegetative buds. Vegetative lateral buds are 3-5 mm long (Figs. 21, 22) and the embryonic shoot within the bud is only about 1 mm long and green (Fig. 11). There is considerable variation in size of vegetative buds and the enclosed embryonic shoots because of differences in vigour of the buds and of the shoots on which they are borne.

FIGURE 29. Scanning electron micrograph of a dormant pollen cone after bud scales were removed. Apical meristem (A) and microsporophylls with two microsporangia (M) are shown. (X 15)

FIGURE 30. Median longitudinal section of a dormant pollen cone showing the microsporophylls bearing microsporangia (M) which contain pollen mother cells (PMC). (X 15)

Seed-cone buds are most easily recognized by their erect position on the upper surface of vigorous shoots and by their large size (Figs. 23, 24). Dormant seed-cone buds are larger than other buds, dome-shaped to conical, brown, and encased by a layer of resin (Figs. 23, 24). Seed-cone buds have about the same number of bud scales as vegetative buds but the bud is as broad as the receptacle to which the bud scales attach. Seed-cone buds are 7-10 mm long and the embryonic cone within is 3-4 mm long (Figs. 27, 28) and green. Embryonic seed cones are deeply buried in the receptacle (Fig. 27), making bud scales difficult to remove to observe the cone. Embryonic

seed cones are distinct because of their large size and many pointed bracts (Fig. 28). Variation can occur in size of seed-cone buds because of differences in vigour of the shoots on which they are borne. Amabilis fir tends to have larger seed-cone buds than the other two species, but otherwise they appear similar.

Pollen-cone buds are easily recognized because they occur abundantly all along the lower surface of shoots of lower vigour (Fig. 25) below the seed-cone region of the tree. Dormant pollen-cone buds are smaller than seed-cone buds and most lateral vegetative buds. They are round or dome-shaped, brown, and encased by a thin layer of resin (Fig. 26). They have only approximately 10 to 15 bud scales. The receptacle is small and the embryonic cone is perched on top of the receptacle (Fig. 26). This makes the buds easy to dissect, but because they are weakly attached to the shoot they are easily broken off during dissection. Many latent buds are usually found among the pollen-cone buds. Often all potential pollen-cone buds will become latent and appear similar but smaller than well-developed pollen-cone buds. However, latent buds will contain only very small apices rather than large pollen cones. Consequently, a sample of pollen-cone buds should be dissected (Fig. 26) to insure that they have developed fully. Dormant pollen-cone buds are 2-3 mm long and the embryonic cone within is only 1-2 mm long and green to red (Fig. 26) (Owens and Molder 1977*b*; Eis and Craigdallie 1981; Owens and Singh 1982).

Forecasting Cone Crops

The abundance of cone buds varies from year to year and it is often useful to estimate in the fall the abundance of cones that might be available for pollination in the spring and for cone collection the next fall. In true firs, this estimate often can be made in September after cone buds have developed enough to be identified easily. Earlier identification is difficult, especially for seed-cone buds. Bud dissection is also necessary to distinguish vegetative lateral buds from seed-cone buds, and latent buds from pollen-cone buds.

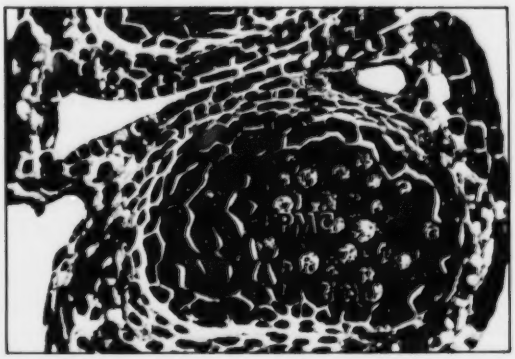


FIGURE 31. Section of a dormant microsporophyll showing the pollen mother cells (PMC) within the microsporangium. (X 170)

Because the production of pollen cones and seed cones is usually closely correlated on a tree, it is easier to forecast the cone crop based on counts of the more easily recognized pollen-cone buds. Sample branches collected from the middle pollen-cone bearing portion of the crown can be sampled from several trees. The presence of well-developed rows of pollen-cone buds on the lower surface of shoots (Fig. 25) can be determined quickly. Also, sample pollen cones can be dissected (Fig. 26) or sliced down the centre to determine the proportion of pollen-cone buds that have fully developed. Collections of sample seed-cone bearing branches from the upper branches in the crown of true firs are usually not practical unless sample trees are felled or topped.

If one tree in a particular location bears many cone buds, this does not insure that all trees in that area

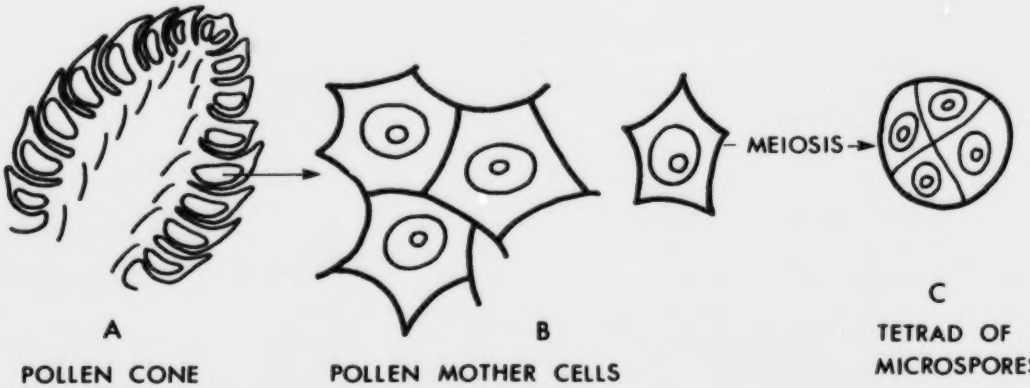


FIGURE 32. Pollen development after winter dormancy.

have abundant cone buds. Individual trees appear to have their own cycle of cone production, which may be modified by climate. In any location there are usually some trees bearing abundant cone buds. Therefore, an adequate sampling of trees in an area is necessary for an accurate forecast of potential cone crop to be carried out. Generally, an abundant cone crop in one fall means there likely will be few cones on the same trees the next fall (Powell 1977*b*). Development of many seed cones during the summer appears to inhibit the development of most seed-cone buds in that same tree. Therefore, few seed cones will be present the next year. It should be emphasized that bud counts made in September can forecast accurately the absence of a cone crop, but not necessarily the abundance of a cone or seed crop. Frost, cone abortion, poor pollination, insects, and disease can seriously reduce potential cone and seed crops between September, when cone buds can be recognized, and one year later, when seeds are shed (Fig. 7) (Dobbs *et al.* 1976; Eis and Craigdallie 1981).

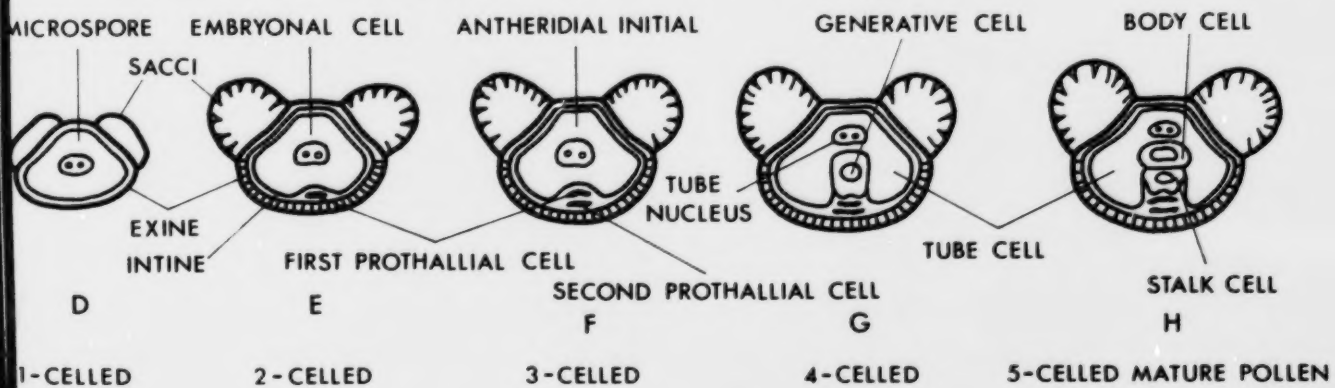
Pollen-Cone Development

All microsporophylls are initiated rapidly during the first month of pollen-cone bud development (Fig. 17). Then, each microsporophyll forms two "microsporangia" (pollen sacs) on its lower ("abaxial") surface. Sporogenous cells form in each pollen sac; they divide and form many large, angular pollen mother cells ("PMC") before the pollen-cone buds become dormant. Each pollen-sac is lined with a single layer of cells, the tapetum, which encloses the mass of PMC's (Fig. 31). The pollen-cone buds overwinter at this stage (Figs. 29, 30). Pollen-cone buds of alpine fir become dormant in mid-October and those of amabilis and grand fir become dormant in November (Owens and Molder 1977*b*; Eis and Craigdallie 1981; Owens and Singh 1982).

Pollen-cone buds resume growth in mid-February in coastal grand fir and in early April in alpine and amabilis firs (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). Pollen cones commonly become purple and as they enlarge, cause the buds to swell. There is then a brief period when pollen sacs swell, causing rapid cone enlargement and the cones to push through the bud scales. This occurs when PMC's undergo meiosis, a special form of cell division. During meiosis each PMC forms four microspores ("tetrad"), each microspore with 12 or half ("haploid") the original 24 chromosomes (Fig. 32*C*). Meiosis is completed in early March in grand fir and by the latter half of April in alpine and amabilis firs. Temperature may affect the time of meiosis. It may occur earlier in a warm spring and later in a cool spring. The microspores in a tetrad separate (Fig. 32*D*), and each develops into a pollen grain (Fig. 32*D-H*).

Microspores are angular at first but later round out. A thick wall forms, consisting of two layers: a thin inner "intine" layer and a thick outer "exine" layer which has a sculptured outer surface. Early in development, the exine separates from the intine at two adjacent areas, forming two air-filled wings ("sacci") on the sunken distal surface of the body ("corpus") of the pollen grain (Figs. 32*D-E*, 33-35). Sculpturing on the exine of the wings is smoother than that on the body of the pollen grain (Fig. 34). During the later stages of pollen-wall development, the cells of the tapetum degenerate and some of their contents ("Ubisch bodies") are deposited on the surface of the exine.

After wings form, the haploid microspore cell divides unequally twice, each time producing a small lens-shaped "prothallial" cell on the proximal side (opposite the wings) (Figs. 32*D-E*, 33). The remaining large cell ("antheridial initial") then divides unequally, producing a small generative cell and a large "tube" cell (Fig. 32*F*). The tube cell stores starch grains and the "generative" cell divides equally, forming a "stalk" cell adjacent to the prothallial cells and a body cell. This forms the mature five-celled pollen grain, which dries and is shed within a few days (Figs. 32*G*, 33). The body cell will form the two male gametes after pollination (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).



Pollen grains from the three true firs are microscopically indistinguishable (Figs. 34-36). *Abies* pollen is large, with large wings set in a deep sinus on the proximal surface. The body is bowl-shaped with a thick exine wall, or "cap", having coarse sculpturing and a distinct triradiate mark on the distal surface (Fig. 34). Wings are thin-walled, air- filled, and have a fine reticulum on this inner surface (Fig. 33). Dry pollen grains have a narrow groove between the wings (Figs. 34-36), which becomes wide when pollen is hydrated and swells (Fig. 33).

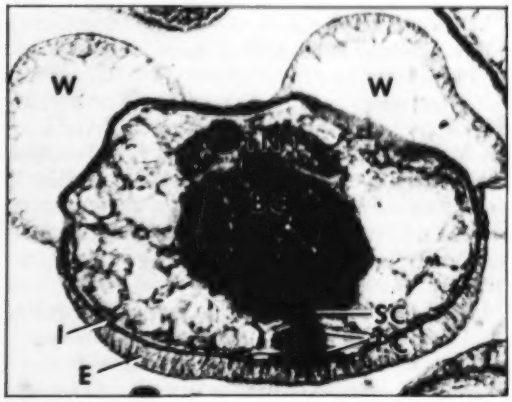


FIGURE 33. Section of mature pollen showing the wings (W), two prothallial cells (PC), stalk cell (SC), body cell (BC), tube nucleus (TN), exine (E), and intine (I). (X 600)

FIGURE 34. Scanning electron micrograph of grand fir pollen showing the two wings, triradiate scar (TS) on the body (B). Arrows show the direction in which the length (L) and width (W) are measured. (X 300)

FIGURE 35. Light micrograph of stained amabilis fir pollen showing wings (W) and body (B). (X 280)

The internal and external structure of the pollen is the same in the three species. Any minute differences in sculpturing are beyond the resolution of ordinary light microscopes. The average size of pollen is different for each of the three species, but the range of pollen size within a species overlaps that of the other two species. Therefore, large samples of pollen and many measurements have to be made to distinguish them. Generally, amabilis fir has the smallest pollen and is long and narrow with a body width and length averaging 43 μm[1] (in a range 28-47 μm) and 75 μm (71-86 μm) respectively.
Alpine fir pollen is larger and broader than long, with the body width and length averaging 75 μm (in a range 71-78) and 66 μm (56-80 μm) respectively. Grand fir pollen is the largest, and is also broader than long, with the body width and length averaging 88 μm (in a range (76-99 μm) and 74 μm (65-80 μm) respectively (Owens and Simpson 1982)[2].

The exposed pollen cones enlarge during pollen development. During the last week or two, as pollen matures and dries, the pollen cones elongate, dry, soften and turn brown. Mature pollen sacs split open as a result of drying. After pollen has been shed, dried empty pollen cones may remain on the tree for many months. To obtain quantities of good pollen, pollen cones should be collected when they begin to dry, soften and turn brown. Purple, wet, firm cones will contain only partially developed pollen, which may not mature properly if the cones are picked. These cones may become mouldy or pollen obtained from them may be immature, wet and inviable. Cones collected after pollen has begun to be shed may contain only small quantities of pollen.

The rate of pollen-cone development after dormancy is greatly affected by temperature, proceeding rapidly during warm weather but slowing during cool or rainy weather. Consequently, considerable variation exists in the time of shedding of pollen in different years and different areas. At low- elevation coastal British Columbia locations, grand fir sheds pollen in mid-April, approximately two months after pollen cone dormancy ends. At moderate elevations in coastal and interior British Columbia locations, amabilis fir and alpine fir shed pollen in late May, approximately six weeks after pollen-cone dormancy has ended (Owens and Molder 1977b; Singh and Owens 1981, 1982). At higher elevations amabilis and alpine firs may not shed pollen until June.

[1] 1 μm = 1/1000 (0.001) of a millimetre.

[2] J.N. Owens and S.J. Simpson, 1982. Manual of conifer pollen from British Columbia. B.C. Min. For. file report. Victoria, B.C.

Seed-Cone Development

Seed-cone bud development in the three species of *Abies* occurs from mid-July until fall (Fig. 20). During this time all bracts are initiated (Fig. 19). Bracts have a broad base and pointed tip (Figs. 28, 36). Soon after each bract is initiated, it forms a small ovuliferous scale in its axil (Fig. 36). Only bracts at the very base and tip of the cone do not develop ovuliferous scales. The next few bracts above and below these, respectively, develop rudimentary ovuliferous scales which remain sterile. The cone apical meristem initiates a few bracts after dormancy but these do not form ovuliferous scales and are sterile. Occasionally the seed cone apical meristem will initiate a series of leaves after dormancy, forming a very short vegetative shoot from the tip of the seed cone. This shoot will die by fall when the seed cone begins to dry.

FIGURE 36. Scanning electron micrograph of a bract (B), ovuliferous scale (OS), and two ovules (OV) from a dormant grand fir seed cone. (X 70)

FIGURE 37. Scanning electron micrograph of a bract (B), ovuliferous scale (OS), and two ovules (OV) from grand fir at pollination. (X 60)

Fertile ovuliferous scales initiate two ovule primordia before winter dormancy. Ovules are on the upper, "adaxial" surface of the ovuliferous scale and consist of a megasporangium, or "nucellus", in the centre of which forms a single large megaspore mother cell ("MMC"). A ring of meristematic cells develops around the megasporangium (Fig. 36) and will form the integument after winter dormancy. Seed-cone buds overwinter at this stage (Figs. 23, 24, 27, 28). Seed-cone buds of alpine fir become dormant about mid-October and those of amabilis and grand fir become dormant in November (Owens and Molder 1977*b*; Eis and Craigdallie 1981; Owens and Singh 1982).

Seed-cone buds resume growth in late January in coastal grand fir and by late March or early April in alpine and amabilis firs (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). Seed-cone buds become very long during the next several weeks before bursting from their bud scales. During cone-bud enlargement, bracts, ovuliferous scales, and ovules develop rapidly (Powell 1970). Bracts elongate but retain their original shape. Ovuliferous scales become oval and ovules enlarge. The ring of meristematic cells forming the integument primordium develops into a hollow cylinder which overgrows the nucellus (Figs. 37, 40). The integument tips in all three species are similar. They are funnel-shaped but the rim is uneven. A notch usually divides the funnel into an upper and lower flap (Fig. 40). The micropyle or opening into the ovule at the base of the funnel is small and oval. The nucellus is situated just inside the micropyle (Fig. 40). Ovules point down in the erect conelets and the funnels extend below the base of the ovuliferous scale into the spaces between the narrow bases of adjacent bract and ovuliferous scale pairs (Fig. 37). The spirally arranged bract-ovuliferous scale pairs leave a labyrinth of spaces adjacent to the cone axis, down through which pollen can sift.

Pollination

The time of pollination varies with the species, the location, and weather. Pollination is earlier at southern locations and lower elevations and when temperatures are warmer. Consequently, pollination times given are relative (Fig. 7). Pollination in coastal grand fir will normally occur before that of other true firs in British Columbia. This is usually about mid-April (Singh and Owens 1982) but may occur a month later in the southern Interior. Pollination in amabilis fir, growing at moderate elevations in coastal British Columbia, occurs in late May (Owens and Molder 1977*b*). In the southern part of its range, pollination may begin by mid-April (Fowells (compiler) 1965). Pollination in

FIGURE 38. Grand fir seed cone at pollination showing pointed bracts. (X 2.5)

FIGURE 39. Amabilis fir pollen cone at pollination. (X 1.2)

alpine fir, growing at moderate elevations in the interior of British Columbia, occurs in mid-May (Singh and Owens 1981), but because of its broad distribution (Fowells (compiler) 1965) there is considerable variation in this time. Although a tree usually sheds its pollen and is receptive for about one week, there is variation between adjacent trees of the same species. Therefore, pollination commonly occurs over about two weeks in any locality.

Pollen cones are pendant and seed cones are erect at pollination (Figs. 38, 39). After seed-cone buds burst, the cone axis continues to elongate, separating the bracts, which bend back, creating large diamond-shaped spaces between bracts. This exposes the ovules and allows pollen to sift between the bracts to the ovuliferous scales. Pollen adheres to the surfaces

FIGURE 40. Scanning electron micrograph of a bract (B), ovuliferous scale (OS) and ovule (OV) showing the irregular integument tip and micropyle (M) at pollination. (X 110)

FIGURE 41. Scanning electron micrograph of an integument tip which is crimping in, taking pollen (P) into the micropyle (M). (X 150

of the bracts and ovuliferous scales. The funnel-shaped integument tips are flared open and hang down below the base of each ovuliferous scale (Fig. 40). Cells on the inner surface of the funnel secrete minute droplets to which pollen adheres. Some pollen grains may pass directly through the micropyle and land on the nucellus. Other pollen grains collect on the inner surface of the funnel for about one week, then the funnel crimps inward (Fig. 41). This entraps the pollen and brings it closer to the micropyle. The development and infolding of the integument tip occurs whether pollen is present or not. No pollination drops form from the ovules, as they do in some other conifers (Singh 1978).

After the seed cones have been open and receptive for approximately one week, the ovuliferous scales enlarge and fill the spaces between the bracts, thus sealing the cones so that no additional pollen can enter. The ovules enlarge and the nucellus in each

ovule grows toward the micropyle. Pollen entrapped in the funnel, or resting on the nucellar tip, swells but does not germinate for several weeks. Not until the ovule forms egg cells, about mid-June in grand fir and mid-July in amabilis and alpine firs, does the viable pollen germinate. Pollen tubes then rapidly grow into the tip of the nucellus. Several pollen tubes may grow through each nucellus.

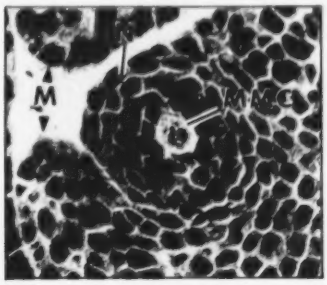


FIGURE 42. Longitudinal section of an ovule from a seed cone after dormancy showing one large megaspore mother cell (MMC) in the nucellus (N). The micropyle (M) is developing. (X 220)

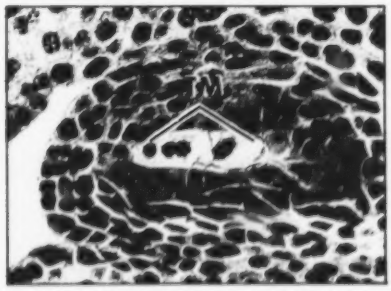


FIGURE 43. Longitudinal section of an ovule showing a linear tetrad of megaspores (TM). (X 220)

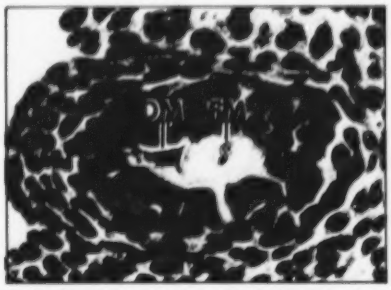


FIGURE 44. Longitudinal section of an ovule showing the degenerated megaspores (DM) and the enlarging functional megaspore (FM). (X 220)

Ovule Development

The female gametophyte tissue, which contains the eggs, develops within the ovule (Fig. 45). After winter dormancy the megaspore mother cell (MMC) in each ovule (Figs. 42, 45*B*) enlarges and undergoes meiosis. Meiosis of the MMC occurs before pollination: in early April in grand fir; mid-April in alpine fir; and in early May in amabilis fir. Despite differences in phenology between the three species, development is the same. Meiosis produces four megaspores, each with half the original 24 chromosomes. Megaspores form a linear tetrad and the middle two megaspores are not separated by a cell wall (Figs. 43, 45*C*). The three outer megaspores degenerate and the inner, functional megaspore (Figs. 44, 45*D*) develops into the female gametophyte (Fig. 49). Development of the female gametophyte takes about two months in grand fir and about two weeks longer in amabilis and alpine firs (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

The functional megaspore enlarges, becomes vacuolate (Fig. 44) and begins a series of free nuclear divisions. An irregular, sac-like free nuclear female gametophyte forms, consisting of a thin parietal layer of multinucleate cytoplasm around a large central vacuole (Figs. 45*E*, 46). The female gametophyte is bounded by a megaspore cell wall which later thickens

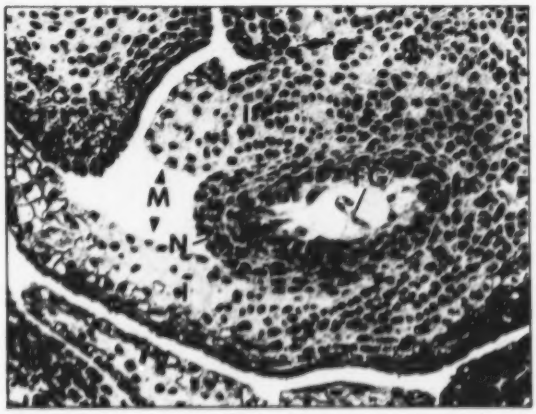


FIGURE 46. Longitudinal section of an ovule at pollination showing the micropyle (M), integument (I), nucellus (N) and free nuclear female gametophyte (FG). (X 120)

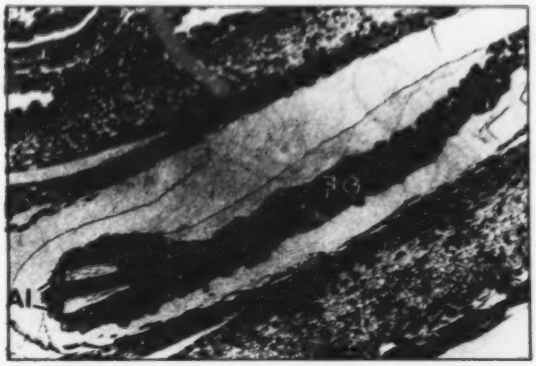


FIGURE 47. Longitudinal section of a portion of an ovule showing the cellular female gametophyte (FG) containing two archegonial initials (AI) inside the nucellus (N) and integument (I). (X 80)

(Fig. 45*F-G*) and becomes sculptured much like the wall of the pollen grain. Outside the megaspore wall is a spongy tapetum which degenerates during female gametophyte development (Fig. 45*F-G*), thus adding to the thickness and sculpturing on the surface of the megaspore wall.

The sac-like free nuclear female gametophyte (Fig. 45*E*) enlarges, then cell walls form, dividing it into many large cells. Most of these cells divide to form smaller cells. At the micropylar end of the female gametophyte several cells do not divide, but enlarge and function as archegonial initials (Figs. 45*F*, 47). Several small cells form an archegonial jacket around each of the archegonial initials. Each archegonial initial then divides unequally, producing a small primary neck cell at the micropylar end and a large central cell (Figs. 45*G*, 48). The primary neck cell divides to form two or more layers of several neck cells per layer. Many large vacuoles form in the central cell giving it a frothy appearance (Figs. 45*G*, 48). The vacuoles become filled with large and small inclusions, called proteid bodies. The central cell then divides unequally, forming a small ventral canal cell adjacent to the neck cells, and a large egg cell. The egg cell nucleus moves to the centre of the egg and the female gametophyte is then mature and ready for fertilization (Figs. 45*G*, 49). Ovules each contain only two to three archegonia in these three species (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). This low number is common in *Abies*.

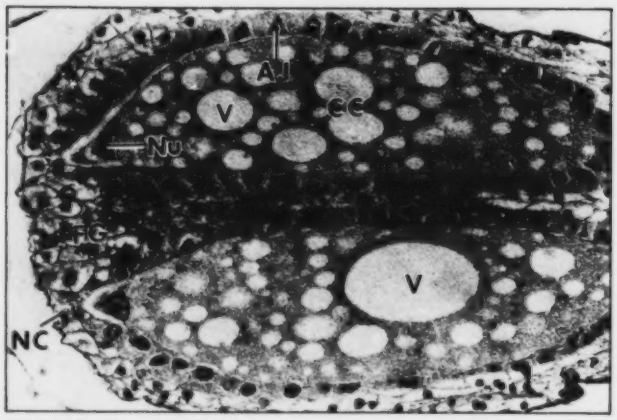


FIGURE 48. Longitudinal section of part of a female gametophyte (FG) showing two developing archegonia. Each archegonium consists of neck cells (NC), archegonial jacket (AJ), and a large central cell (CC) containing a nucleus (Nu) and several large vacuoles (V). (X 180)

The time between pollination and when female gametophytes are mature and ready for fertilization is one month in alpine fir, six weeks in amabilis fir, and two months in grand fir (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). As with many other developmental events, conifers inhabiting areas where the growing season is long take longer for comparable

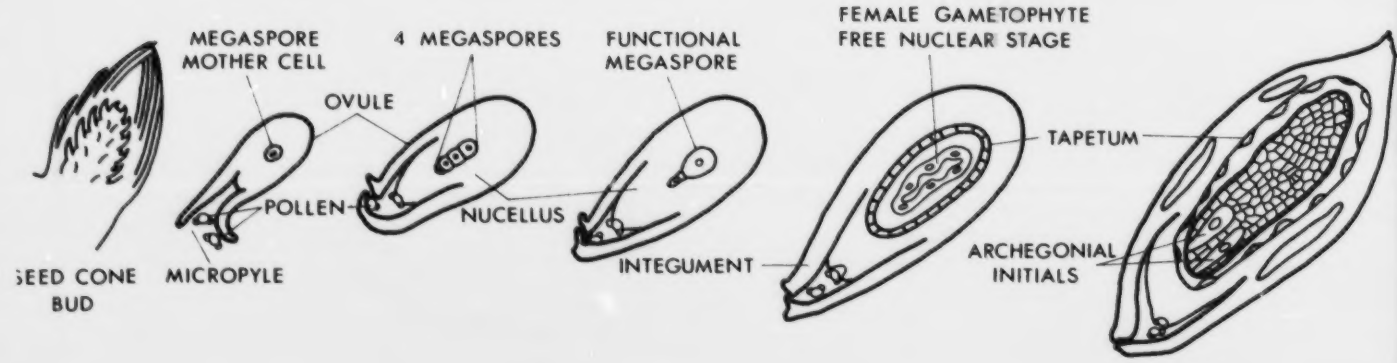


FIGURE 45. Female gametophyte development.

FIGURE 49. Longitudinal section of part of a female gametophyte (FG) and nucellus (N) containing two mature archegonia. Neck cells (NC), archegonial jacket (AJ), ventral canal cell (VCC), egg nucleus (EN), megaspore cell wall (MCW). (X 90)

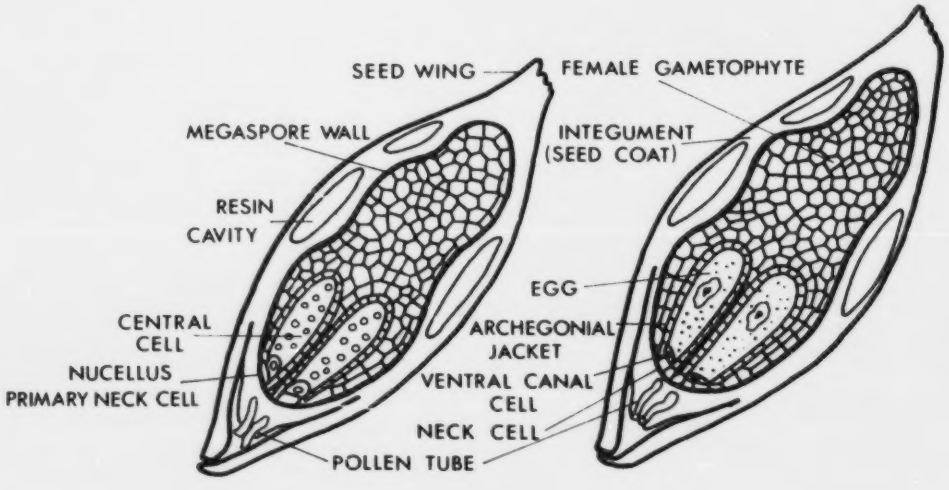
structures to develop than similar species inhabiting areas where the growing season is shorter.

During female gametophyte development the seed cones and their ovules (Fig. 45) rapidly enlarge to their mature size, store abundant food reserves, and develop seed wings from the ovuliferous scales. During the later stages of female gametophyte development, the seed coat differentiates from the integument of the ovule, and the ovules and seed wings separate from the ovuliferous scales, but are held in place in the tightly closed cones. At this stage the eggs within the ovules are ready to be fertilized. Ovules and developing seeds apparently receive no further food reserves from the cone after fertilization. Similar development occurs in other true firs (Miyake 1903; Hutchinson 1914; Singh 1978).

Fertilization

In all three species the pollen in the ovule swells but does not germinate until only a few days before the female gametophyte is mature. Pollen may germinate in the micropyle, in the micropylar canal (between the micropyle and the nucellus), or in the tip of the nucellus. Pollen tubes grow toward the nucellus and cause a breakdown of nucellar tip cells. Several pollen grains may germinate in each ovule and several pollen tubes may grow through each nucellus. Pollen tube growth is very rapid in *Abies*, taking only a few days compared with several weeks in many other conifers (Singh 1978).

As the pollen tubes grow through the nucellus, the body cell, which is carried along in the advancing



pollen tube, divides to form two male gametes, one larger than the other.

When pollen tubes reach the female gametophyte, only one pollen tube penetrates the neck cells of each archegonium (Fig. 50*A*). The contents of the pollen tube are released into the egg cell, leaving a receptive vacuole in the egg cytoplasm (Fig. 50*A*).

The two male gametes lack any visible means of movement, but despite this, the larger male gamete moves through the egg cytoplasm and fuses with the egg nucleus (Figs. 50*A*, 51). The smaller male gamete and other contents of the pollen tube degenerate. Pollen tubes that did not penetrate an archegonium also degenerate.

Fertilization occurs in mid- to late June in alpine and grand firs and mid-July in amabilis fir. All eggs within an ovule may not be fertilized. Unfertilized eggs degenerate within one to two weeks. Lack of fertilization is very common in true firs and may result from either inadequate amounts of pollen reaching the ovules or from poor pollen tube growth. Pollen or pollen tubes need not be present and fertilization need not occur for the ovule to develop into a full-sized seed. However, if no eggs are fertilized within an ovule, the female gametophyte will degenerate, leaving a normal-appearing but empty seed (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

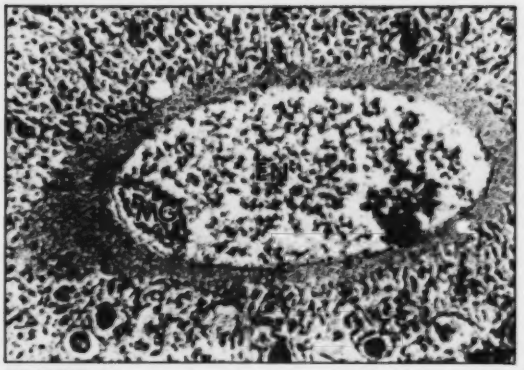


FIGURE 51. Section of an egg at fertilization showing the male gamete (MG) fusing with the egg nucleus (EN). (X 350)

Embryo Development

As in other conifers, embryo development in true firs is separated into two phases: a short proembryo phase that occurs within the archegonium (Fig. 50*A-D*); and an embryo phase that occurs after the proembryo has grown out of the archegonium and into the female gametophyte tissue (Fig. 50*E-F*) (Foster and Gifford 1974; Singh 1978).

Proembryo development begins when the fertilized egg nucleus divides first into two (Fig. 50*A*), then four free nuclei, all contained within a dense region of neocytoplasm in the centre of the egg cell. The neocytoplasm and the four free nuclei then migrate to the end of the egg cell opposite the neck cells. The nuclei become orientated into a single tier (Fig. 50*B*), then each nucleus divides and cell walls form between the eight nuclei to form two tiers of four cells each (Fig. 50*C*). The four cells in each tier divide again to form a 16-celled proembryo consisting of four tiers of four cells each (Fig. 50*D*). The proximal "open tier" remains open to the egg cytoplasm and apparently functions to absorb nutrients stored in the egg. The adjacent "rosette tier" has no known function, but in some conifers may divide and form small clumps of cells — often mistakenly called "rosette embryos". These cells soon degenerate. The next tier of cells,

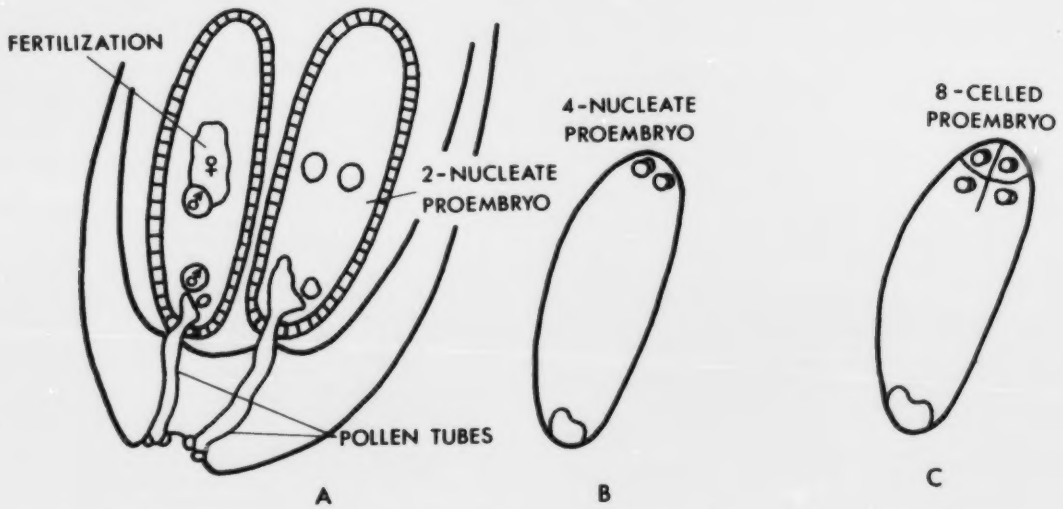


FIGURE 50: Fertilization and embryo development. Stages *H* and *I* show cleavage polyembryony, which occurs in only 20% of developing embryos. (A) Apical cells; (e^1, e^2) embryonal tubes; (S) suspensors.

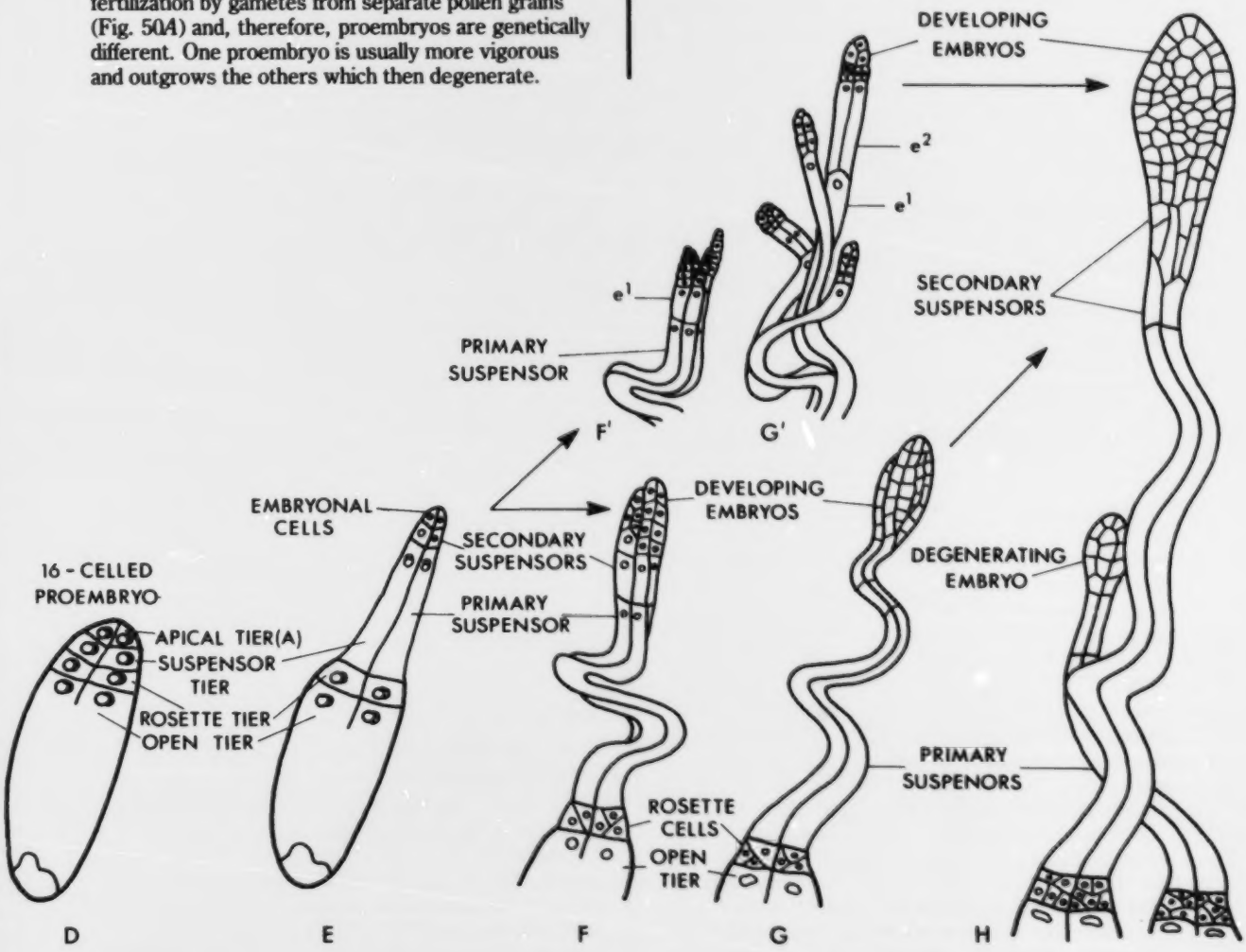
the "suspensor tier", elongates and pushes the distal "embryo tier" through the archegonial jacket and into the female gametophyte tissue (Fig. 50*E*). This ends the proembryo stage, which in these three conifers lasts only a few days (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

The stage that follows is the early embryo stage (Fig. 50*F-H*). During this stage, cells of the embryo tier divide to form distal apical cells and basal embryonal tubes. Embryonal tubes elongate, become coiled, and force the apical cells further into the female gametophyte (Fig. 50*F*).

True firs, like most conifers, undergo two types of polyembryony, the process by which several embryos may develop within one ovule (Foster and Gifford 1974; Singh 1978). "Simple polyembryony" occurs when more than one egg is fertilized within an ovule (Fig. 50*A*). All three of these true firs have only two to three eggs (each one within an archegonium) per ovule and more than one egg may be fertilized. Each resulting embryo could develop into a mature embryo. In simple polyembryony, each embryo is a result of fertilization by gametes from separate pollen grains (Fig. 50*A*) and, therefore, proembryos are genetically different. One proembryo is usually more vigorous and outgrows the others which then degenerate.

The second type of polyembryony, "cleavage polyembryony", occurs in only 10-20% of the *Abies* ovules. Cleavage occurs when the suspensor tier elongates and embryonal tubes form. Cleavage refers to the separation of the apical cells into four files of cells (Fig. 50F^1), each of which can develop into a separate but genetically identical embryo (Foster and Gifford 1974; Singh 1978). As with simple polyembryony, usually one of these embryos resulting from cleavage is more vigorous and the others soon degenerate (Fig. 50G^1). In a true fir ovule having three eggs, all of which become fertilized, three proembryos could form by simple polyembryony. In turn, each proembryo could form four embryos by cleavage polyembryony. Consequently, 12 young embryos may begin to develop if cleavage polyembryony occurs.

Most *Abies* species do not have cleavage polyembryony (Singh 1978) and only one embryo develops from each fertilized egg. That is, all four cells of the apical tier remain together and usually



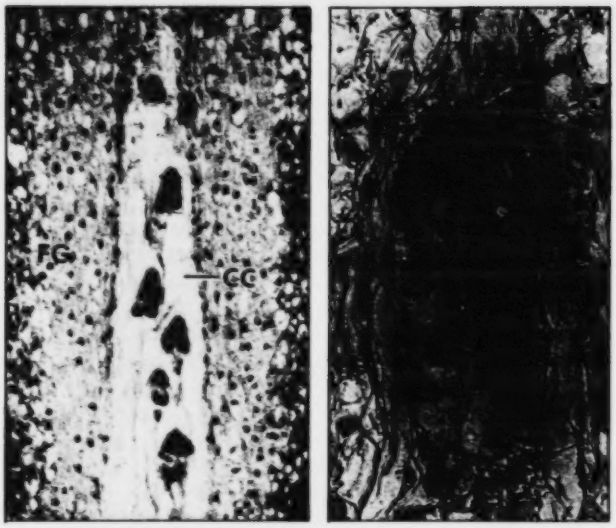


FIGURE 52. Longitudinal section of an ovule showing five early embryos developing in the corrosion cavity (CC) in the female gametophyte (FG). (X 70)

FIGURE 53. Close-up of an early embryo. Cells in the right half (arrow) are overgrowing those of the left half of the embryo. (X 300)

contribute equally to the embryo. However, one or more apical cells may divide more frequently than the others, overgrow the others (Fig. 54), and contribute more to embryo development. This type of development has been called "delayed cleavage polyembryony", even though complete cleavage does not occur (Singh 1978). In this case, all apical cells do not contribute equally to the embryo (Fig. 54), making this stage of embryo development quite variable in the true firs. It is uncertain how important delayed cleavage polyembryony is in embryo development, in *Abies* as well as in the other genera — such as *Picea* (spruce) and *Pseudotsuga* (Douglas-fir) — where it occurs (Allen and Owens 1972; Owens 1973; Owens and Molder 1984*b*).

Regardless of the aforementioned variations, mature *Abies* seeds seldom have more than one mature embryo. All other embryos stop development at a very early stage, degenerate, and are reabsorbed. In the early embryos, which continue to develop, apical cells at the tip of the embryonal tube cells (Fig. 50*E*) divide many times and form a small club-shaped embryo (Figs. 50*G-H*, 55). The suspensor cells and embryonal tubes elongate and become coiled as they push the club-shaped embryo to the middle of the female gametophyte (Figs. 50*H*, 55). Here the embryo enlarges rapidly (Fig. 56).

Cells at the distal end of the embryo form several "cotyledons" (embryonic leaves) around a small shoot apical meristem. The root apical meristem forms in the central portion of the embryo. The more basal cells form a thick secondary suspensor. At this stage, the developing embryo is suspended at the end of the secondary suspensor in the centre of the female gametophyte, the seed is fully enlarged, and the seed coat is hardening (Fig. 56). This stage is reached in early July in grand fir, and in late July in amabilis and alpine firs (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

During the next four to six weeks embryos and seeds mature, the "hypocotyl" (embryonic shoot) and cotyledons elongate, and provascular tissue appears. A massive root cap develops from the root apical meristem but the shoot apical meristem remains small and inactive (Fig. 57) (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

During embryo development, stored food is dissolved and a region of clear cells is left around the embryo (Figs. 52-56). These female gametophyte cells degenerate, forming a corrosion cavity in which the embryo develops (Fig. 56). The remaining female gametophyte cells contain stored food in the form of starch and lipo-protein which change as the embryo matures (Figs. 56, 57) (Owens and Molder 1977*b*; Singh and Owens 1981, 1982).

FIGURE 54. Close-up of a later stage of the early embryo. Cells on the right side have overgrown the lightly stained cells on the left. (X 300)

FIGURE 55. Longitudinal section of an ovule showing the surviving embryo just before meristematic zones appear. Inner female gametophyte (FG) cells are collapsing next to the corrosion cavity (CC). (X 70)

Seed Development

The seed coat (testa) begins to differentiate from the integument about the time of fertilization, and differentiation is completed in August in all three species. The integument differentiates into three layers: (1) an outer layer, which is thin and dark and fused with the seed wing; (2) a hard, thick middle layer of thick-walled cells; and, (3) a thin inner layer (Singh 1978). A thin papery layer of nucellar tissue lies

lies inside the seed coat. This is prominent only at the micropylar end of the seed where it forms a thick pad of tissue (Fig. 58). A very thin megaspore cell wall is firmly attached to and encloses the female gametophyte (Fig. 58).

Resin cavities develop in the outer layer of the seed coat during seed development (Figs. 56, 60) (Owens and Molder 1977*b* ; Singh and Owens 1981, 1982). Enlargement of these cavities causes depressions in the surface of the female gametophyte and causes the mature seed coat to become somewhat spongy. Each resin cavity is lined with secretory cells that produce the resin. Resin cavities are characteristic of *Abies* seeds but uncommon in other conifer seeds.

A seed wing develops from the ovuliferous scale and is attached to the end of the seed opposite the micropyle (Fig. 59). At about the time of pollination (Fig. 37), the seed wing begins to develop from the surface cells of the ovuliferous scale and by the time of fertilization, when seed cones are fully enlarged, a

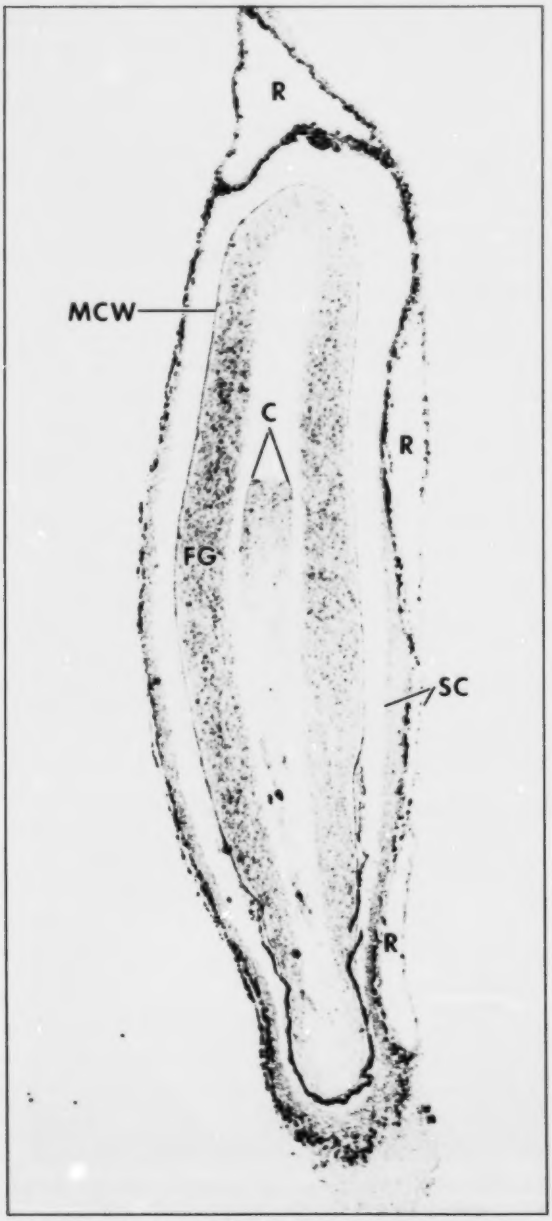


FIGURE 56. Longitudinal section of an ovule in mid-summer showing the embryo within the corrosion cavity at the time of cotyledon (C) initiation. Female gametophyte (FG), megaspore cell wall (MCW), seed coat (SC), and resin cavities (R). (X 20)

FIGURE 57. Longitudinal section of a mature seed with seed coat removed showing the embryo in the female gametophyte (FG). Cotyledons (C), shoot apical meristem (SA), root apical meristem (RA), root cap (RC), and hypocotyl (H). (X 25)

seed wing two to three cells thick has formed. At this time, a separation layer forms beneath the ovule and seed wing. Complete separation of the seed and seed wing from the ovuliferous scale occurs during early stages of seed development.

In dry mature seeds, the embryo is loosely packed within the rather firm, white nutritive female gametophyte tissue, often called "endosperm". Seeds carefully sliced with a sharp razor blade (Fig. 60) show most of the detail described for thin sections of seeds. Sliced dry seeds can be used to monitor embryo and seed development (Dobbs *et al.* 1976). Hydrated seeds are poor for this purpose because the contents swell and obscure the boundaries of the different tissues.

Seed development is completed late in August in all three species. This is about three months after pollination in alpine and amabilis firs (Fig. 7) and four months after pollination in grand fir. Some changes may occur within seeds as cones dry and seed is shed.

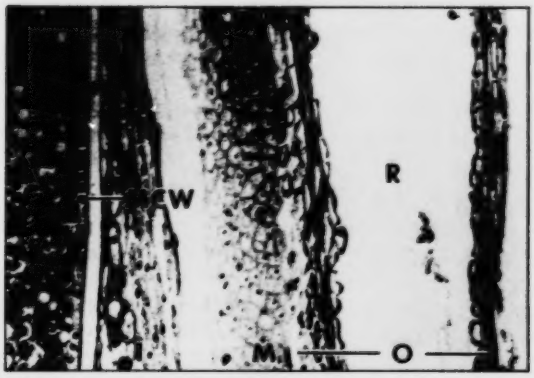


FIGURE 58. Section of a portion of the female gametophyte (FG), megaspore cell wall (MCW), and seed coat, showing inner (I), middle (M), and the outer (O) layer which contains the resin cavity (R). (X 70)

Cone Maturation, Seed Release, and Regeneration

In the three species, 14-15 months elapse between the time of cone bud initiation and when seed cones are mature and seeds begin to be shed. Pollination, fertilization, and seed development occur in the second growing season (Fig. 7). True fir seed cones remain erect throughout development and do not open to shed their seed. Rather, as cones mature and dry in late summer, an abscission layer, similar to that at the base of a leaf, forms at the base of each bract and ovuliferous scale. The bract-ovuliferous scales, often with both seeds attached, are shed, leaving the cone axis as an erect spike on the branch. Spikes will remain for a year or more, giving an indication of the abundance of recent cone crops.

FIGURE 59. Mature seeds, with seed wings attached, of alpine fir (left), grand fir (middle) and amabilis fir (right). Scale on left is in millimetres.

Cones begin to disintegrate and shed seeds in early September, and most seed is shed by the end of October in the three species (Foiles 1959; Fowells (compiler) 1965). However, considerable variation may occur in the time when seeds are shed, depending upon the weather. Dry warm weather in late summer may cause earlier shedding of the seed. Wet cool weather may delay the process.

The true firs have large cones each with many ovuliferous scales and many seeds. Ovules at the base and tip of the cone either do not develop, or develop more slowly than ovules from the central portion. Ovules whose development is slowed or arrested usually remain as small flat seeds that contain no female gametophyte or only a poorly developed one. These seeds have small seed wings. Ovules from the central, fertile portion of the cone also may abort during early development and also form flat seeds. Ovules that are not pollinated or not fertilized form normal-looking but empty seeds. This occurs because pollen is not required for normal female gametophyte and ovule development. Pollen is required for this development in some other conifers (Singh 1978). An empty seed contains no embryo and only a shrivelled female gametophyte (Fig. 60) that aborted after the time when fertilization would normally occur. A

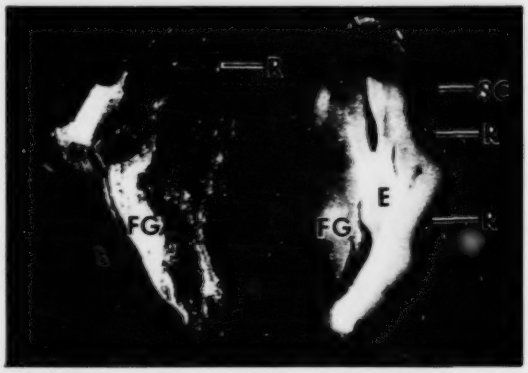


FIGURE 60. Mature alpine fir seeds sliced longitudinally. Filled seed on right shows the embryo (E), female gametophyte (FG), and seed coat (SC) containing several shiny resin cavities (R). Seed on left looks normal externally but contains a shrivelled female gametophyte and no embryo. (X 5)

developing embryo is needed to prevent the female gametophyte from aborting. Filled but inviable seeds result from incomplete embryo development or seeds damaged after maturation. Normal viable filled seeds contain well developed embryos (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). More elaborate classifications of types of seeds produced, based on seed development, have been devised (Dogra 1967).

The seeds of the three species are large compared with many other conifers (Fig. 61). Amabilis fir seeds are the largest with about 33 000 cleaned seeds per kilogram. Grand fir has about 48 000 and alpine fir about 106 000 cleaned seeds per kilogram (Dobbs *et al.* 1976). Considerable variation can occur in seed size within each species (Fowells (compiler) 1965; Franklin 1974).

Dissemination of seeds is mostly by wind. Because the seeds of the three species are large and because seeds may adhere to the ovuliferous scales, seeds are seldom carried far (Fowells (compiler) 1965). Some seed may be distributed up to 120 m from the parent tree but most falls within approximately 60 m of the

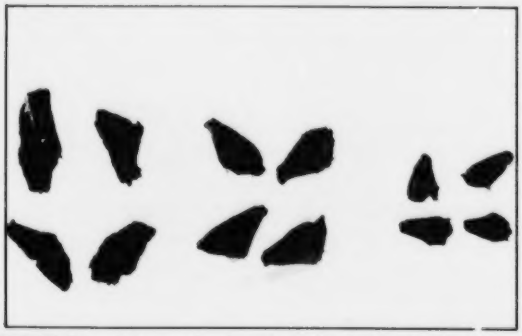


FIGURE 61. Mature dewinged seeds of alpine fir (left), grand fir (middle) and amabilis fir (right). (X 1)

parent tree. Dissemination of seeds by birds and small mammals is probably insignificant (Foiles 1959).

These three true firs, like most other true firs, are only moderate seed producers. Although many seeds are produced in these large cones, not many cones are produced per tree and moderate to good cone crops occur infrequently compared with other competing conifers (Fowells (compiler) 1965). The major problem in true firs is the generally high per cent of empty seed produced (Franklin 1974). The reasons for the high per cent of empty seeds is uncertain but inadequate pollination is frequently suggested. Inadequate pollen, especially at higher elevations, may be a factor as well as the inefficient pollination mechanisms. These, coupled with the precise timing of pollen-tube development to coincide with the completion of female gametophyte development, would result in infrequent fertilization. This could lead to a high frequency of empty seed. Several insects also can harm or destroy *Abies* seeds and cones at various stages of development (Franklin 1974; Hedlin *et al.* 1980).

Seeds disseminated in the fall may germinate in the spring after one overwintering period. True fir seed relative to others, is fragile because the large resin cavities in the seed coat result in a thinner hard middle layer at that point.

The large seed may result in a large seedling with a vigorous root system. Seedlings become established on a wide variety of natural seedbeds, are relatively resistant to drought, and are shade tolerant. However, heavy shade results in very slow growing seedlings which may not survive subsequent drought because of poor root development. Seedling growth, especially in alpine and amabilis firs, is relatively slow for several years and they may not compete well with many associated species (Foiles 1959; Fowells (compiler) 1965; Franklin 1974).

Cone Collection, Seed Extraction, Storage, and Germination

The proper time for cone collection is important and will vary with the species, site, and weather from year to year. It is recommended that a sample of cones be collected from several trees in an area and that these cones be cut longitudinally to determine the number of filled seeds per half-section of cone. This will provide an estimate of the number of filled seeds per cone. If adequate cones and filled seeds are present, samples of cones should be taken periodically to determine seed maturity (Dobbs *et al.* 1976; Edwards 1980). For true firs, sample cones should be taken at least weekly starting in August (Owens and Molder 1977*b*; Singh and Owens 1981, 1982). Seed maturity can be estimated by seed cutting tests, where individual seeds are removed from cones, seeds are sliced longitudinally (Fig. 60), and the development estimated by the per cent elongation of the embryos (Dobbs *et al.* 1976). Cones should be collected when embryos have reached over 95% of their potential length (Fig. 60) and the female gametophyte tissue is white and firm, with little shrinkage from the seed coat.

Cone colour is not necessarily a good indicator of seed maturity in true firs. Cones that prematurely and irregularly turn brown are usually insect damaged and should not be collected. True fir cones must be collected before they turn brown because, at that time, ovuliferous scales will begin to be shed and seeds may be lost. Seed and wing colour are reliable maturity indices. Immature seeds and wings are nearly white to transparent. As seeds mature the wing tips turn purple and both seed and wings may turn light brown. At this stage they more easily separate from the scale[1]. The essential early collection of true fir cones, before they are fully mature, requires

[1] British Columbia Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

that they be stored in cool, well-ventilated areas to promote further ripening and control moulding which may occur in cones having high moisture content (Dobbs *et al.* 1976). Embryos will complete development and seeds will mature in properly stored cones. Immature cones that are dried too quickly may case-harden and not open. If they do open, their seeds may be immature and not viable. The very resinous nature of true fir cones and seeds makes handling difficult (Leadem 1980).

The present procedure followed in British Columbia for true fir seed storage is to briefly store cones in burlap bags, out-of-doors in a covered area. This is usually followed by tray storage in a forced-air chamber at 5-18°C[1]. Cones should be stored for at least six weeks, up to several months, prior to processing, during which time the seeds mature, the cones dry, ovuliferous scales abscise, and seeds are released. In general, the longer the period of cone storage, the better is the quality of the seeds as long as good storage conditions exist. Cones allowed to get wet may become mouldy and ruin seed.

True fir cones are not kiln dried because high temperatures cause resinous cones, scales, and seeds to become sticky. Disintegrated cones may be gently shaken to separate seeds from the ovuliferous scales. Harsh tumbling may damage the seed coat and resin vesicles. Resin may cause ovuliferous scales to adhere to one another and seeds to adhere to the ovuliferous scales. Leaving cones to mature and slowly dry under cool dry temperatures causes the resin to harden and become much less sticky. This allows for easier handling of cones and seeds during the winter. Excessive resin often results from insect damaged cones and seeds[1].

Seeds are usually dewinged by hand or gentle tumbling in a cement mixer. Care must be taken to ensure that damage does not occur to the seed coat or resin vesicles. Dry seeds having a moisture content of less than 10% may be stored at -19°C in air-tight bags for several years without significant decrease in viability[1]. True fir seeds stored at room temperature in open containers retain little or no viability after one year (Franklin 1974).

Seed dormancy in true firs appears to be both physiological and physical. Placing the seeds in cool moist conditions ("stratification") breaks the dormancy, possibly by physiologically changing inhibitors and by physically changing the seed coat (Franklin 1974). Recommended stratification for true fir seed involves placing moist seeds at 2°C for two months before sowing. In some instances a stratification-redry process may result in better germination[1]. Seeds are soaked in water for 24-48 hours at 1°C, stratified at that temperature for one month at 40% moisture content, then dried to 30% moisture content, and stratified at 0 to 2°C for three months before sowing. The redrying and stratification at 30% moisture content allows seeds to mature without germinating. Many *Abies* seeds stratified at 40% moisture content will germinate even at near freezing temperatures. The lower moisture content prevents this premature germination[2]. Germination tests are made for 28 days under 8 hours of light at 30°C and 16 hours of darkness at 20°C[1]. These procedures differ somewhat from official seed analysis rules for testing seeds or other pregermination treatments (Franklin 1974).

[1] British Columbia, Ministry of Forests, Seed Centre, personal communication, 1982, Duncan, B.C.

[2] Dr. Carole Leadem, personal communication, 1982, British Columbia Ministry of Forests, Research Branch, Victoria, B.C.

The Seedling

Seed germination occurs by the elongation of the embryonic root ("radicle") and embryonic shoot (hypocotyl) (Fig. 57). This forces the root out of the micropylar end of the seed. The hypocotyl elongates and forces the cotyledons out of the ground, usually carrying the seed coat with them. The cotyledons may vary in number from three to 12 depending upon the species. The small apical meristem located at the tip of the stem, just above the cotyledons, initiates a spiral series of leaf primordia and new stem tissue. The stem and the primary root elongate throughout most of the growing season. Lateral branch apical meristems may be initiated in the axils of some leaves.

FIGURE 62. One year old grand fir seedling. (X .75)

These lateral branches may elongate and form several leaves before they form a winter bud (Fig. 62). Lateral or branch roots form from the primary or tap, root and these in turn branch, usually forming an extensive root system under favourable soil, nutrient, and temperature conditions.

As days become shorter in the summer, seedling growth slows and the apical meristem of the terminal and lateral shoots form a series of bud scales followed by a series of leaf primordia. The bud scales enclose the embryonic shoot and these structures constitute the vegetative bud which will resume growth, flush, and elongate after winter dormancy. It is normally only during the first growing season of the seedling that free growth will occur. Free growth is when leaf primordia and stem tissue elongate and mature immediately after being initiated. It occurs in all conifer seedlings during the first year's growth. Seedlings of some conifers may have a period of free growth in the spring for several years, but this does not appear to be common in true fir seedlings.

With the formation of terminal and axillary buds in the fall of the first growing season, the pattern of vegetative bud and shoot development becomes established. In subsequent years, vegetative buds normally pass through the same cycle of winter dormancy, bud-scale initiation, lateral bud initiation, leaf initiation, and winter dormancy as was described for vegetative buds of mature trees (Fig. 8).

Summary

At least one of the three true firs (alpine fir, amabilis fir, and grand fir) can be found in almost all regions of British Columbia. Alpine fir is most widely distributed throughout most of the Interior and in coastal mountains. Amabilis fir occurs at moderate elevations along the coast, whereas grand fir is restricted to the low-elevation southern regions of the province. Despite their wide distribution, they are only of moderate economic importance and are used most extensively for pulp.

The three species are taxonomically distinct but each shows close affinities and overlaps in distribution with other true firs.

The reproductive cycles of the three species are essentially the same. The phenology of vegetative and reproductive development is very similar in alpine and amabilis firs that inhabit sites where the growing season is approximately seven months long, April through October. Coastal grand fir has an eight- to nine-month growing season, consequently, the time at which developmental events occur — very early and late in the growing season — differs from the other two species. However, the phenology of events occurring during late spring and in summer are about the same in all three species. Phenology differs the most in alpine fir, which inhabits more extreme geographical and elevational habitats.

The reproductive cycles of the three species extend over 14-15 months from the time of cone-bud initiation in the summer, until seeds are shed in the fall of the second year. True firs have a long juvenile period of growth when no cones are produced. As in most conifers, cone initiation occurs the first year, then cone buds overwinter. The initiation of cone buds is very cyclic within a tree, with many cone buds being initiated only every few years. As in most conifers, the most common cause of a poor cone crop is the failure to initiate cone buds. However, factors that affect cone-bud differentiation in true firs are poorly understood. Unlike some conifers, cone induction or enhancement in true firs have seldom been tried and have not been obtained by cultural or chemical means.

Pollination, fertilization, and ovule and seed development occur in the second year. During that time, many environmental and physiological factors may affect cone and seed development. Generally, true firs have a low percentage of filled seed. The most likely causes of this are the lack of pollination or fertilization. The pollination mechanism is very unspecialized and relatively inefficient in true firs. Since true fir ovules do not require pollen to be present in order for the ovules to develop, many normal-appearing but empty seeds are produced. The development of the pollen tube and ovule are more highly synchronized in true firs than in most other conifers. Consequently, any asynchrony results in no fertilization and empty seeds. These factors, along with the very cyclic cone-bud initiation, contribute significantly to the low cone and filled seed production often encountered in true firs.

Added to these internal factors are the many environmental factors that may be encountered at the higher elevation sites or northern regions where amabilis and alpine fir commonly grow. The effects of low temperatures and adverse weather at different developmental stages are not known. These could affect cone initiation, which is enhanced by high temperatures and low rainfall, as well as pollination which is generally poor in rainy weather. Cone bud and subsequent cone abortion may also be affected by climate.

True fir cones and seeds must be handled differently than those of other conifers. Disintegration of the cones necessitates early collection and ripening of picked cones. The resinous seed coat requires careful handling to prevent injury to the seeds which can slow or prevent germination. Seed and cone insects are also a common problem in true firs.

Many factors that adversely affect cone initiation and cone and seed development can be avoided, overcome, or minimized in trees that are grown in carefully managed seed orchards. Under these conditions, more frequent crops of abundant high-quality seeds may be obtained from selected parent trees. Understanding the complete reproductive cycles of alpine, amabilis, and grand firs is a first, essential step in enhancing and controlling cone and seed production for reforestation of these conifers.

References

Allen, G.S. and J.N. Owens. 1972. The life history of Douglas-fir. Environ. Can., Can. For. Serv. Ottawa, Ont.

British Columbia Ministry of Forests. 1982. 1981 annual report Statistical Supplement. Victoria, B.C.

Dallimore, W. and A.B. Jackson. 1966. A handbook of Coniferae and Ginkgoaceae. St. Martin's Press, New York, N.Y. Revised by S.G. Harrison.

Dobbs, R.C., D.G.W. Edwards, J. Konishi and D. Wallinger. 1976. Guideline to collecting cones of B.C. conifers. B.C. For. Serv. and Can. For. Serv., Joint Report No. 3.

Dogra, P.D. 1967. Seed sterility and disturbances in embryogeny in conifers with particular reference to seed testing and tree breeding in Pinaceae. Stud. For. Suec. 45: 1-97.

Edwards, D.G.W. 1980. Maturity and quality of tree seeds — a state-of-the-art review. Seed Sci. and Technol. 8: 625-657.

Eis, S. 1970. Reproduction and reproductive irregularities of *Abies lasiocarpa* and *A. grandis*. Can. J. Bot. 48: 141-143.

Eis, S. and D. Craigdallie. 1981. Reproduction of conifers: a handbook for cone crops assessment. Environ. Can., Can. For. Serv., Report BC-X-219.

Foiles, M.W. 1959. Silvics of grand fir. U.S.D.A. For. Serv. Intermountain For. Range Exp. Stn., Ogden, Utah, Misc. Pub. No. 21.

Foster, A.S. and E.M. Gifford, Jr. 1974. Comparative morphology of vascular plants. W.H. Freeman, San Francisco, Cal.

Fowells, H.A. (compiler). 1965. Silvics of forest trees of the United States. U.S.D.A. For. Serv., Wash. D.C. Agric. Handb. No. 271.

Franklin, J.F. 1968. Cone production by upper-slope conifers. U.S.D.A. For. Serv., Pac. Northwest For. and Range Exp. Stn. Res. Pap. PNW-60.

_____. 1974. *Abies* Mill. Fir. *In* Seed of woody plants in the United States. C.S. Schopmeyer (editor). Agric. Handbook No. 450. U.S.D.A. For. Serv., Wash. D.C., pp. 168-183.

Hedlin, A.F., H.O. Yates III, D.C. Tovar, B.H. Ebel, T.W. Koerber and E.P. Merkel. 1980. Cone and seed insects of North American conifers. Environ. Can., Can. For. Serv., Ottawa, Ont.

Hosie, R.C. 1969. Native trees of Canada. Environ. Can., Can. For. Serv., Ottawa, Ont.

Hunt, R.S. and E. Von Rudloff. 1974. Chemosystematic studies in the genus *Abies*. I. Leaf and twig oil analysis of alpine and balsam firs. Can. J. Bot. 52: 477-487.

_____. 1979. Chemosystematic studies in the genus *Abies*. IV. Introgression in *Abies lasiocarpa* and *Abies bifolia*. Taxon 28: 297-305.

Hutchinson, A.H. 1914. The male gametophyte of *Abies*. Bot. Gaz. (Chicago) 57: 148-153.

Leadem, C. 1980. Seed viability of *Abies*, *Picea* and *Tsuga* after storage in the cones. *In* Proc. International Union of Forest Research Organizations. Int. Symp. Forest Seed Storage, Petewawa Nat. For. Inst., Chalk River, Ontario, pp. 57-67.

Miyake, K. 1903. Contribution to the fertilization and embryogeny of *Abies balsamea*. Beih. Bot. Centralbl. 14: 134-144.

Murray, A. 1863. On the synonymy of various conifers. Roy. Hort. Soc. Proc. 3: 308-325.

Owens, J.N. 1973. The reproductive cycle of Douglas fir. Environ. Can., Pac. For. Res. Cen., Can. For. Serv., Victoria, B.C.

_____. 1984. Bud development in grand fir (*Abies grandis*). Can. J. For. Res. 14: 575-588.

Owens, J.N. and M. Molder. 1977*a*. Vegetative bud development and cone differentiation in *Abies amabilis*. Can. J. Bot. 55: 992-1008.

_____. 1977*b*. Sexual reproduction of *Abies amabilis* (Dougl.) Forbes. Can. J. Bot. 55: 2653-2667.

_____. 1984*b*. The reproductive cycles of western and mountain Hemlocks. B.C. Min. For., Info. Serv. Br. Pub., Victoria, B.C.

_____. 1984*b*. The reproductive cycle of interior spruce. B.C. Min. For., Info. Serv. Br. Pub., Victoria, B.C.

Owens, J.N. and H. Singh. 1982. Vegetative bud development and the time and method of cone initiation in subalpine fir (*Abies lasiocarpa*). Can. J. Bot. 60: 2249-2262.

Parker, W.H., G.E. Bradfield, J. Maze and S.C. Lin. 1979. Analysis of variation in leaf and twig characters of *Abies lasiocarpa* and *A. amabilis* from north-coastal British Columbia. Can. J. Bot. 57: 1354-1366.

Parker, W.H. and J. Maze. 1984. Intraspecific variation in *Abies lasiocarpa* from British Columbia and Washington. Amer. J. Bot. 71: 1051-1059.

Powell, G.R. 1970. Postdormancy development and growth of microsporangiate and megasporangiate strobili of *Abies balsamea*. Can. J. Bot. 48: 419-428.

_____. 1974. Initiation and development of lateral buds in *Abies balsamea*. Can. J. For. Res. 4: 458-469.

_____. 1977*a*. Initiation and development of subterminal buds in *Abies balsamea*. Can. J. For. Res. 7: 258-262.

_____. 1977*b*. Biennial strobilus production in balsam fir: a review of its morphogenesis and a discussion of its apparent physiological basis. Can. J. For. Res. 7: 547-555.

Puritch, G. 1972. Cone production in conifers: a review of the literature and evaluation of research needs; with an economic analysis by A.H. Vyse. Environ. Can., Pac. For. Res. Cen., Can. For. Serv., Victoria, B.C. Info. Report BC-X-65.

Ross, S.D., R.P. Pharis and W.D. Binder. 1983. Growth regulators and conifers: their physiology and potential uses in forestry. *In* Plant growth regulating chemicals. L.G. Nickell (editor). CRC Press, Boca Raton, Fla., Vol. 2: 35-78.

Singh, H. 1978. Embryology of a gymnosperms. Borntraeger, Stuttgart, W. Germany.

Singh, H. and J.N. Owens. 1981. Sexual reproduction in subalpine fir (*Abies lasiocarpa*). Can. J. Bot. 59: 2650-2666.

_____. 1982. Sexual reproduction in grand fir (*Abies grandis* Lindl.). Can. J. Bot. 60: 2197-2214.

Von Rudloff, E. 1975. Volatile leaf analysis in chemosystematic studies of North American conifers. Biochem. Syst. Ecol. 2: 131-167.

_____. 1976. Chemosystematic studies in the genus *Abies*. II. Leaf oil analysis of grand fir. Can. J. Bot. 54: 1926-1931.

Von Rudloff, E. and R.S. Hunt. 1977. Chemosystematic studies in the genus *Abies*. III. Leaf and twig oil analysis of amabilis fir. Can. J. Bot. 55: 3087-3092.